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The Ecology of the Phytoplankton of a New Reservoir  
in the Thames Valley

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by

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### Abstract

A three-year investigation of the phytoplankton and associated physical and chemical environmental factors of the River Thames and the Queen Elizabeth II reservoir is described. In addition to routine analyses and records, the methods to be employed were critically surveyed and some were modified before regular use. A new method of particle counting and sizing involving the use of a Coulter Counter is described and the results compared in detail with those results obtained by other means. The influence of artificially imposed turbulence - a unique condition restricted to this reservoir - on the thermal conditions and on the phytoplankton is considered. The importance of the quality and the quantity of the River Thames inflow is discussed. Culture experiments are described which indicate that  $\text{SiO}_2$  might at times be a limiting nutrient for the growth of diatoms in the River Thames and the reservoir. Culture experiments also indicate perennation, especially by certain diatoms, in the reservoir sediment.

The Ecology of the Phytoplankton of a New Reservoir in  
The Thames Valley

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## Chapter I

### Introduction

The increase in demand for potable water, for industrial needs as well as human consumption, and the subsequent inadequacy of the ground water supplies, has prompted the utilisation and management of both rivers and lakes. The gradual increase in the use of polluted water in some areas and the development of storage reservoirs has, therefore, been inevitable.

Bleasdale and his associates (1962) considered that storage reservoirs fall into three different categories, based on their construction and method of construction and their eventual use.

These categories are:-

- 1) Direct supply impounding reservoirs in which the water is piped, usually under gravity, to the points of consumption.
- 2) River regulating reservoirs which are used, primarily, to maintain the flow of river downstream, and abstraction of water for consumption is some distance from the reservoir.
- 3) Intake or pumped storage reservoirs which are built in a geologically suitable site, but without adequate catchment areas.

Law (1966) considered that 'the amount of storage required to maintain a specified yield is dependent upon the characteristics of the river from which the reservoir is fed or which it regulates, but in general there is a law of rapidly diminishing returns for the greater storage provided....'

In many reservoirs, the development of thermal stratification in the summer and the marked changes in the biological and chemical conditions of the water which can accompany this stratification, are often the major source of trouble in the maintenance of the specified yield.

Many reservoirs in the world today are the result of direct impoundment of the river course e.g. Slapy reservoir in Czechoslovakia (Hrbáček 1966) the damming of natural valleys e.g. Chew Valley reservoir in England (Hammerton 1959) or the improvement of existing water bodies e.g. Lake Arplich (Meshkova 1960 in Langhelt M.Sc. Thesis 1968). The nature of the biota in these reservoirs ranges from purely riverine to lacustrine, with many in-between grades and is dependent on both the morphometry and the water throughput of the reservoir.

The acute need for storage reservoirs in south-eastern England and in particular within the immediate vicinity of London and its conurbation, has resulted in the construction of several reservoirs, belonging to the third category [of types], in the Thames Valley. These reservoirs, entirely man-made, are largely lacustrine in nature, although they differ from natural bodies of water in several respects. These include the absence of rooted marginal vegetation, the reduced benthic zone of algae and their initial elevated construction with clean gravel bottoms and no silt deposits.

As a result of the eutrophic and highly polluted nature of the River Thames and its tributaries which form the feeder system for these reservoirs, they serve the additional purposes of sedimentation basins and sites of preliminary but natural bacterial purification.

The construction of some of the Thames Valley reservoirs since the beginning of this century has been described by Ridley (1962) but he continues 'It would appear that in Britain there has been little or no application of the fundamental limnological principles either to the design or to the use of storage reservoirs'. However, the realisation of the importance of algae, in particular phytoplankton in these storage reservoirs (see for example Pearsall et al 1946) has resulted in a marked increase in limnological investigations into water supplies (see for example Lund 1954, 1966, Lowe-McConnell 1965, Hrbáček 1966). Although there have been several such investigations in the Thames Valley reservoirs, it is only recently, in the construction of the Queen Elizabeth II reservoir that the information has been applied to reservoir design (see Ridley 1962).

There has been a large amount of published work concerning the many aspects of phytoplankton ecology; including the patterns of seasonal succession and the associated changes in environmental factors, in natural and semi-natural bodies of fresh water (see for example reviews in Lewin 1962, and by Ruttner 1963, Lund 1965 and Hutchinson 1967). However as Lund (1965) comments "Little is



known for certain about the detailed reasons for... changes which can be observed in phytoplankton.'

Detailed ecological studies of river and more especially perhaps, reservoir phytoplankton, potentially result in reciprocal benefits both to our fundamental knowledge, and the many applied aspects of hydrobiology.

#### The Queen Elizabeth II reservoir

The general construction of the Thames Valley reservoirs has been described by Ridley (1964). The Q.E.II reservoir, the most recently constructed reservoir in this system, was completed in 1962 and has been maintained in continuous service since 1963. This reservoir is situated in Walton-on-Thames, Surrey, approximately 1 mile from the River Thames intake which is just below the Sunbury Lock. Its position and size, relative to the other Thames Valley reservoirs in the area is shown in fig 1. An irregular pentagon in shape, 317 acres (128 hectares) in area and with a maximum depth of 57.5 feet (17.5 metres), the Q.E.II reservoir has a maximum storage capacity of  $4.3 \times 10^9$  gallons. Thus, although this reservoir has a smaller capacity than either the Queen Mary (see Ridley 1962) or the King George VI reservoirs, it is, at present, the deepest reservoir in the system.

The artificial circulation in the Q.E.II reservoir is not only induced by the continual throughput of water which ranges from  $30 \times 10^6$  to over  $120 \times 10^6$  gallons per day, but also by an unique

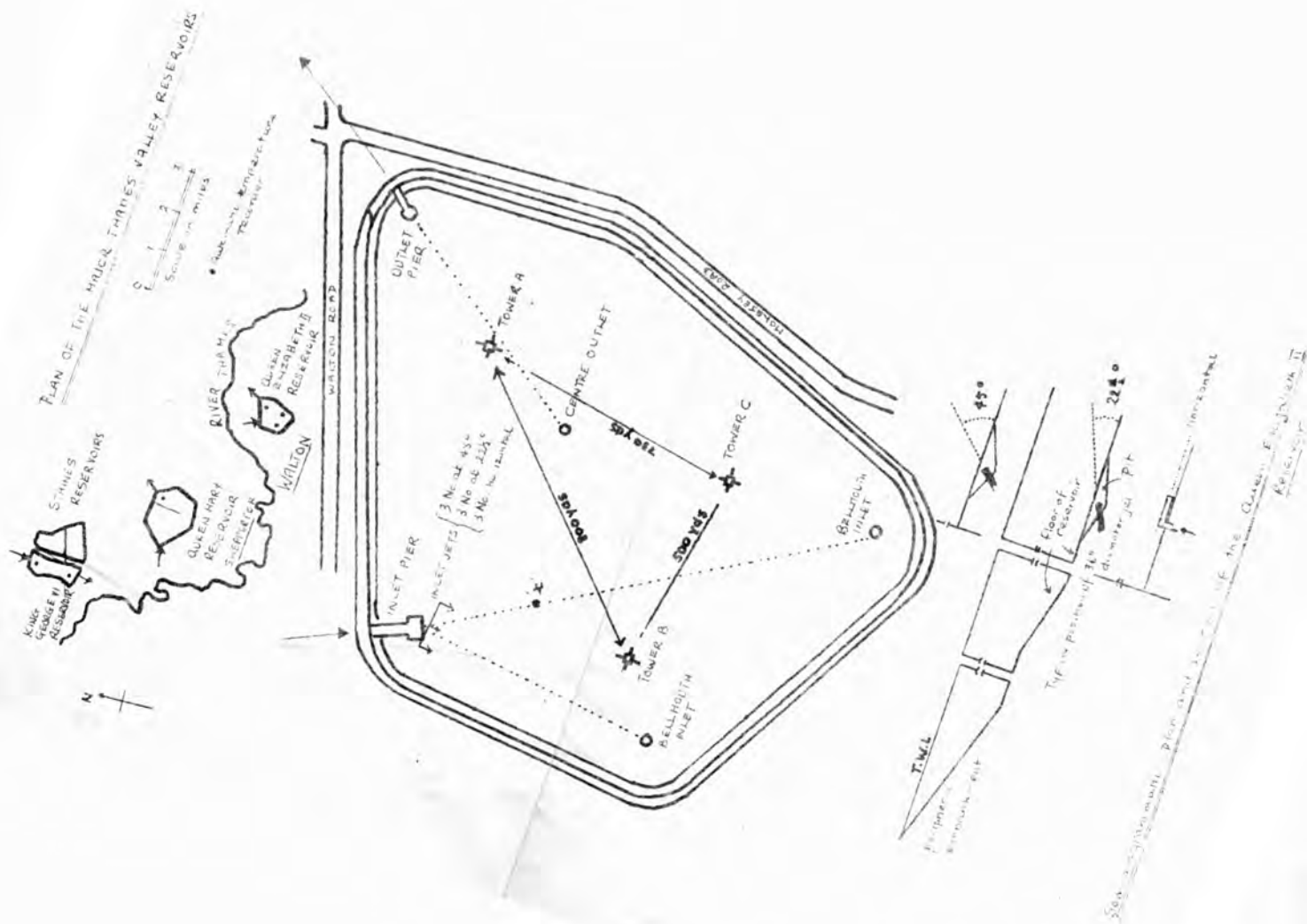
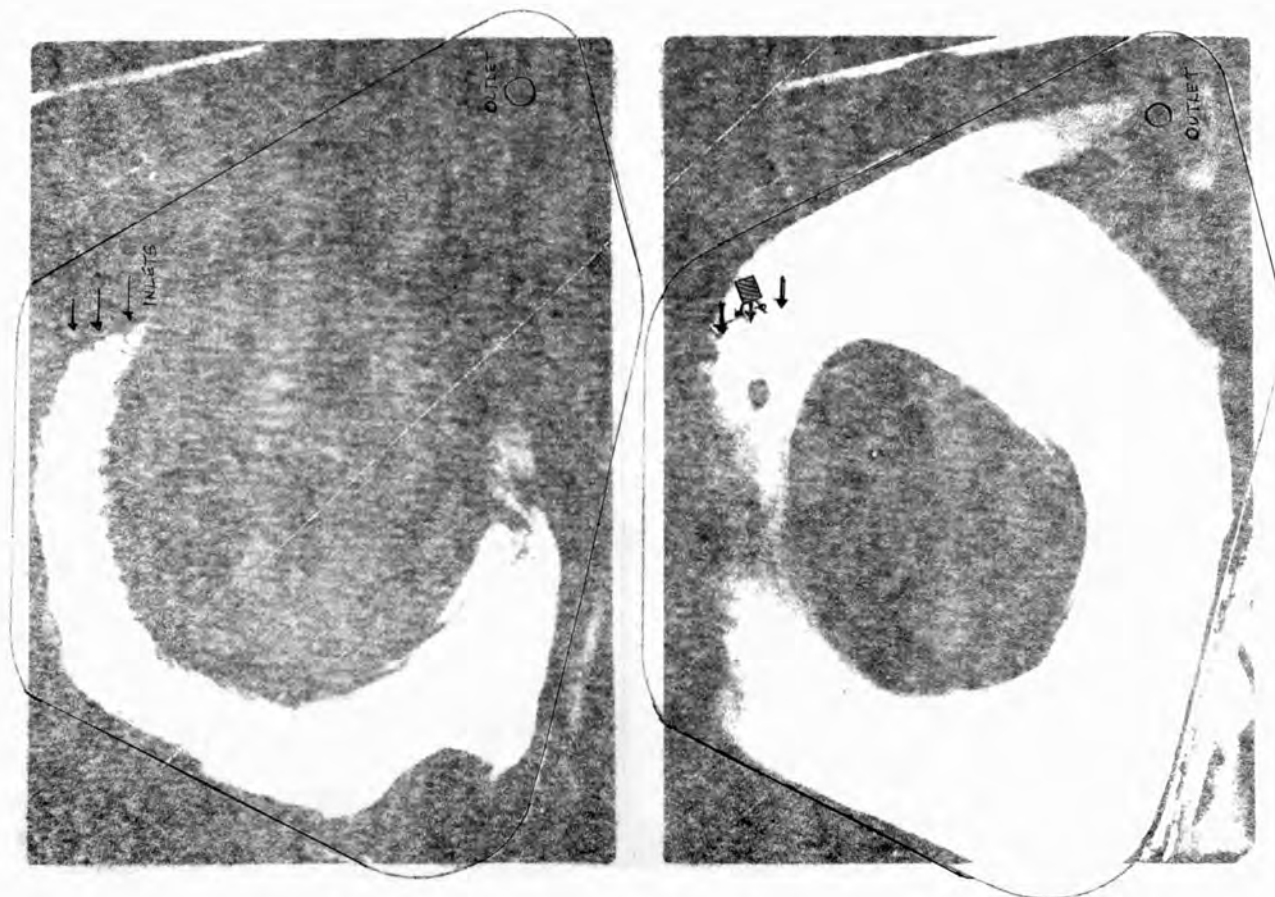


Figure 1

Figure 1 cont.d.



Walton Reservoir 1:300 model. Penetration of new water after 6.5 and 26 hours (prototype), 5 and 20 mins. (model). Three horizontal 36 in. inlet pipes at bottom of berm. Intake density 0.165% (prototype), 3.3% (model) less than water in reservoir. (taken from White C.H., Harris S.L. and Cooley P. 1955 unpublished)



system of high velocity inlets in addition to conventional low velocity Bellmouth inlets. The circulation, particularly the vertical entrainment of water, induced by these well-like Bellmouth inlets situated in the floor of the reservoir (see fig 1 ) is dependent on both the density difference between the inflowing river water and the impounded reservoir water and on the rate of throughput. The entrainment is, theoretically, greatest when the influent is less dense than the impounded water so that the upwelling is maximal, but in reality, this is much modified by the existing thermal conditions in the reservoir. The circulation induced by the high velocity 'jet' inlets, which are situated at the shoreline in the north-west corner of the reservoir (see fig 1 ) is however, largely independent on the density gradient between the influent and impounded waters, and much less influenced by the thermal conditions in the reservoir. The design and position of these inlets, based on the theory of jet dispersion, followed mainly the recommendations of White and his associates (1955) after their experimental work on scale-models of the reservoir, (see Cooley and Harris 1954). Their orientation and position in the reservoir is such that the nine jets composed of three series inclined at  $0^{\circ}$ ,  $22\frac{1}{2}^{\circ}$  and  $45^{\circ}$  to the floor of the reservoir induce an approximately circular flow pattern in the reservoir. The injection of river water through these inlets promotes both vertical and horizontal entrainment of the

impounded water, and this is most effective when a combination of inlets is used. The use of the  $45^{\circ}$  inclined inlets in projecting the influent to the surface is maximal in the promotion of vertical entrainment, but its range is limited to a small area as its horizontal entrainment is slight. The action of the horizontally inclined inlets in promoting water entrainment is the reverse, resulting in maximal horizontal movement. Although the maximal overall turbulence is perhaps induced by the  $22\frac{1}{2}^{\circ}$  inlets, their action and thus effectiveness, may be modified by the existing thermal conditions. Some of the principles involved in the induction of artificial turbulence by these inlets are discussed more fully by Ridley, Cooley and Steel (1966).

The circulation of water within the Q.E.II reservoir is further modified by the existence of two outlets. These are situated in the floor, near the centre of the reservoir and in the north-east corner where the water can be drawn from several depths.

In the present investigation into the phytoplankton of this relatively new reservoir during 1966 to 1969 an attempt has been made to compare these organisms in relation to the artificial circulation induced by this unique inlet system, outlined above.

In addition to more or less regular routine analyses of the phytoplankton and some of the major chemical and physical environmental factors, several other aspects of possible limnological interest have been followed.

From the methodological aspect of phytoplankton ecology, a preliminary study of an electronic particle-counting instrument - the Coulter Counter - has been made (see Evans and McGill 1969, and also in publication). The use of this instrument in measuring biomass has been linked with studies of other parameters, such as total algal volume, calculated from direct visual counts; and sestonic dry weight, organic matter and algal pigments. An attempt has been made also to follow the growth and survival of certain algae by culture techniques.

## Chapter II

### Methods

Preliminary samples were collected regularly from the reservoir from November 1965 until May 1966 to investigate the seasonal changes in the dominant species in the phytoplankton and variations in sampling and analytical methods.

In agreement with the staff of the Metropolitan Water Board and to fit in with their sampling procedure, a regular (usually weekly) routine sampling programme at selected sampling stations in the reservoir and at the river inlet was started in July 1966 and maintained until May 1968. At the same time the methods of analysis described below were adopted with the exception of that for the extraction and determination of phytoplankton pigments. Routine analysis for these pigments was not started until April 1967 and a small change in the procedure for sample analysis was made to accommodate it. (See page 15)

### Collection of Samples

Routine collection of samples were made by the staff of the Metropolitan Water Board (M.W.B.) during their own regular sampling programme. A Friedinger water sampler was used for depth sampling throughout and part of each Friedinger sample (approximately 1.2 litres) was available for this study. All non-routine samples were collected by the author.

Weekly samples for the reservoir from November 1965 until April 1966 were taken at each of the three observation towers and both the inlet and outlet piers (see Fig. 1 Map of reservoir). Each station, except the outlet pier was sampled at the surface and at three depths, 1 metre (m), 9 metres and at about one metre above the bottom of the reservoir. Samples from the outlet pier were taken from the taps within the laboratory which were connected directly to the reservoir by small bore pipes some 80 feet in length and the inlets of which were situated very close to the pier (see page for map) at depths of 3.3m (10 feet), 6.6m (20 feet), 9.9m (30 feet), 12.2m (40 feet) and 16.5m (50 feet). In April 1966, sampling at Tower C and at the inlet pier were discontinued, but a similar series of surface and depth samples were taken from an additional station - x - nearer the centre of the reservoir. After July 1966, no further samples were taken from the outlet pier via the taps in the laboratory and until May 1968 only the three main stations at Towers A and B and site x were sampled. During this period, the number of depth samples in the routine weekly collection was increased to seven so that, at each station, samples were taken at the surface, 1m, 3m, 5m, 9m, 13m, and at about one metre above the bottom of the reservoir.



As soon as the samples had been returned to the laboratory, the preliminary treatments of preservation and filtration were carried out. From November 1965 until July 1966, each sample was treated individually but from August 1966 until October 1966, the filter residues of equivalent depth samples were combined while the filtrate for each sample was still analysed separately.

In October 1966 until May 1968, all equivalent depth samples were added and mixed together before the preliminary treatment to give, finally, seven depth samples each of approximately 3.6 litres.

The decision to mix all equivalent depth samples was based on the assumption that in an investigation into a new environment it is important to gather as much information as possible on every facet of that environment. To do this, it is necessary that all the parameters investigated should be directly comparable. Similarly a plankton population is best described by several rather than a few parameters. Thus by mixing and combining samples it has been possible to analyse both the seston and the dissolved nutrients in the reservoir, throughout the seasons. However, it is probable that the seven depth samples used, although representative of the samples collected, were not completely representative of the reservoir as a whole.

Preliminary research into the artificial turbulence induced by the jetting inlet system on a scale-model of the Q.E.II reservoir (Cooley 1954) suggested a circulation pattern shown in fig 1. The towers were built within the main circulatory path but there were apparently stagnant areas in the middle of the reservoir and around the outlet pier. The prevailing wind, assisting the surface circulation, blows in a north east direction into the outlet area. The sampling stations used for the main part of the study therefore do not cover both areas of stagnation although station x is possibly on the edge of the stagnant middle area.

Sampling from the outlet pier was not continued throughout the study, since the laboratory tap inlets were situated at different depths from which the main reservoir samples were taken, and therefore could not be considered comparable.

Before these sampling sites were chosen an attempt was made to collect representative samples with a small-bore plastic hose with continuous suction. The hose was towed behind a small dingy with an outboard motor and several samples were taken across the reservoir. However it was not possible to maintain the hose at a particular depth and therefore, although the horizontal variation in samples was reduced, it was impossible to get representative depth samples. The technique was not successful and discrete depth samples were used instead.

Samples of inflowing river water were taken at weekly intervals from late 1965 until May 1968, in the inlet channel at the entrance to the Walton Pumping Station. Apart from the latter period of this investigation, from early 1968, most of the river samples were collected personally. One sample (with occasional duplicates as checks) of 1-3 litres was collected from mid-channel just below the surface of the water each week. It was considered that one sample would be representative of the inflow since there were apparently well mixed turbulent conditions throughout the channel. Such conditions were perhaps to be expected since the channel is small (maximum width and depth less than 20 feet and 10 feet respectively) while the daily total volume of inflowing water is large (usually greater than 100 million gallons per day (m.g.d.)). However preliminary observations on the total particulate volume of the suspended seston in a series of samples ~~(see table)~~ collected along the channel confirmed this turbulence since the seston was apparently similar in volume in all the samples. Also the volume of the suspended matter at the river intake, in a sample collected at the same time as the series along the channel, was similar to that found in the channel. From this it was assumed that the routine weekly sample could be considered to reflect conditions at the river intake and thus be representative of the river at the time of sampling. From November 1966 until mid-August 1967, samples of the reservoir outflow were collected at filter beds at Surbiton.



All samples were brought back to the Q.E.II reservoir Laboratory where the chemical analyses and the preliminary treatment for seston analyses were carried out as soon as possible and within three hours of collection.

### Analysis of Samples

Before discussing the details of the methods employed during this study a brief description of the development of the procedure of analysis is given:-

In addition to routine analyses carried out by staff of the Metropolitan Water Board regular analyses for dissolved nitrate-nitrogen, nitrite-nitrogen, ammoniacal-nitrogen, phosphate-phosphorus and silicon dioxide (silica) of the reservoir samples were begun in March 1966, and continued until May 1968.

From March until May 1966, each reservoir sample was filtered through treated Whatman GF/C glass fibre pads (see page 34) to remove most of the particulate matter and the filtrate was analysed. At the same time, seston analyses of dry weight, ash free dry weight, oxidizable carbon and total particulate volume were determined on suspended particulate seston in samples collected from the taps within the Laboratory (see page 9). These taps samples were finally discontinued at the end of July 1966, since they were not comparable with the main reservoir samples.

By the end of May 1966, analysis of the suspended particulate matter was started on the filter residues from the reservoir samples; although each filtrate was analysed separately it was necessary to filter equivalent depth samples through a common filter pad in order to obtain measurable quantities of seston.

From October 1966 until May 1968, analysis of the dissolved nutrients and the particulate seston were carried out on the same combined depth sample for each depth.

Determination of the 'chlorophyll a' and algal pigments content of the seston was started in April 1967 and was carried out at fortnightly intervals except during periods of large 'growths' when weekly determinations were made. Since the 'chlorophyll a' content was low during the winter period it was often necessary to use the seston from large volumes of water (up to 5 litres) and this was achieved by one of two ways. Either the 'chlorophyll a' content of each depth sample was determined to the detriment of the analysis of the sestonic organic matter content for that sample, or pigment analysis was carried out on the seston from two or more combined samples. In the latter case the mean chlorophyll content for either the total reservoir (all seven depths samples combined), or for three combined depths - top (surface + 1m + 3m), middle (5m + 9m) and bottom (13m + 16m), or for two combined depths - upper (surface 1m, 3m and 5m) and lower (9m, 13m and 16m) was measured.

Both the dissolved nutrients and the particulate matter analyses were carried out on the river sample each week since a larger volume of sample was available. A plan of the filtration and the pretreatment of the raw water samples before the analyses of the dissolved and the particulate matter is given ~~in Figure~~ on p.34.

### Dissolved Nutrients

Pyrex glassware, precleaned in chrome-sulphuric acid, was used throughout the investigation for all the analyses.

The reagents were made up from Analar-grade chemicals whenever it was possible. They were kept either in a dark cupboard at room temperature or in a refrigerator when not in use.

Since all the chemical methods used were colorimetric a Hilger and Watt 'Spekker' absorptiometer with the appropriate filters was used to determine the optical density of the resultant solutions. Either a reagent blank or distilled water was used as a reference sample and in the latter case an appropriate correction was made for the effect of the reagents.

The raw water samples were standardised at a temperature of approximately 20°C in either an incubator or a waterbath. All the samples were then filtered through glassfibre pads and the filtrates were used in the analyses. Before use, the glass fibre pads (Whatman GF/C. 5cm) were heated at 500°C in a muffle furnace for at least 30 minutes. This pretreatment of the filter pads was necessary since it was shown in preliminary tests that they could each lose up to 2.5mg in weight when 'muffled' although the loss between papers - even of a similar batch, was not standard. These losses were found to be due mainly to a carbon-based filter contained in the papers, some of which was retained even after the heat treatment. This made it necessary to make blank determinations of several papers when analysing the sample residues for the oxidizable carbon (see page 22). This procedure was also

recommended by Strickland and Parsons in their revised edition of 'A Manual of Seawater Analysis' (1966). For easy identification, especially in the determination of particulate organic matter where several weighings were involved, small notches were made in the perimeter of each filter paper before the heat treatment.

#### Ammoniacal - Nitrogen

This was determined by direct Nesslerisation using the method described by Mackereth (1963). It was not necessary to pretreat for natural colour, but 1ml of Rochelle Salt solution was added to the sample just before the addition of 2ml of the Nessler's reagent. This reagent was made up according to the recipe of Williams (1964), and added to 50 ml of sample. The resulting colour was estimated in the 'Spekker' using 601 filters after about 20 minutes to allow for full colour development, against glass distilled water as reference.

A calibration curve was constructed using Ammonium sulphate as a standard.

#### Nitrite - Nitrogen

This method was based on that described by Montgomery and Dimmock (1961).



Sulphanilic acid - Potassium hydrogen sulphate solution

2.17gm of Sulphanilic acid and 17gm of Potassium hydrogen sulphate were dissolved in 500ml of glass-distilled water.

N-Naphthylethylenediamine dihydrochloride

0.1% solution in glass-distilled water.

To 20ml, 25ml or 30ml of each water sample were added 2ml of the Sulphanilic acid reagent and then 10 minutes later 1ml of the N-Naphthylethylenediamine dihydrochloride solution. The sample volume was then made up to 50ml with glass distilled water and the resultant colour, after 20 minutes, was measured using 604 filters in the 'Spekker'.

Sodium nitrite was used as a standard for the calibration curve.

Nitrate - Nitrogen

This method was based on that given by Mackereth (1963) with some of the modifications recommended in A.P.H.A. (1955). Until November 1966, 25ml of sample were used in each determination. Pretreatment with hydrogen peroxide - the modification in A.P.H.A. (1955) - to prevent nitrite interference was necessary before the sample was evaporated to dryness over a waterbath. The colour was developed in alkaline solution after 1ml of Phenoldisulphonic acid had been added to the dried sample. The final solution, adjusted to 50ml, was then determined in the 'Spekker' in a cell of 1cm path length with 601 filters. After November 1966, and for the rest of the period of study, only 5ml of raw sample were used and the

pretreatment was discontinued. The final colour was then measured in a cell of 4cm path length.

Potassium nitrate was used as a standard.

#### Phosphate - Phosphorus

During 1966, the Atkin's modification of Deniges' method which is described by Mackereth (1963) was used. In 1967 the method was then changed to that given by Strickland and Parsons (1960) in which the reducing agent is ascorbic acid. A small modification was made to the reagents since the ammonium molybdate, sulphuric acid and the potassium antimony tartrate were mixed to give a single solution which kept very well. This solution was added to the ascorbic acid in the ratio 4:1 just before use. The colour of the final solution after 5ml of this mixed reagent had been added to 50ml of the water sample, took about 20 minutes to develop. It was measured in the 'Spekker' with a reduced sensitivity and 608 filters. In both methods it was necessary to make the measurements against a reference reagent blank.

#### Silicon dioxide (Silica)

This was taken from the method used at the Metropolitan Water Board in which there is a single reagent added to each sample to produce the coloured silico-molybdate complex.

Acid - Ammonium molybdate solution

200gm of ammonium molybdate were dissolved in about 600ml of distilled water.

200ml of concentrated Sulp uric acid were added to 700ml of distilled water and then cooled.

The ammonium molybdate solution was then carefully mixed with the acid and the resulting solution was then adjusted to 2 litres.

The reagent was kept in a dark bottle.

To 50ml of water sample was added 1ml of the mixed reagent and 20 minutes was allowed for full colour development. The colour was determined with 601 filters in the 'Spekker' against a distilled water reference sample.

An approximate calibration curve was made up with water glass in solution (a mixture of sodium silicate and silicic acid). An independent calibration with pure, fresh sodium silicate crystals agreed very closely with it and it was therefore assumed the results would be sufficiently close to the absolute silicate values for the method, and quite acceptable for comparative purposes.

Dissolved oxygen content of the water was determined by the Staff of the Metropolitan Water Board using either the Winkler technique or a polarographic method. Other chemical data for both the river and the reservoir were taken from the appropriate records in the Annual Reports of the Metropolitan Water Board.



### Particulate Matter (Seston)

Determinations of dry weight, ash-free dry weight (loss on ignition) oxidizable carbon content and 'algal pigments' of the seston were made on the residues from the filtration of the raw water samples. In most samples the residues consisted of suspended silt and organic debris as well as plankton. No attempt was made to separate these components before filtration although afterwards the larger Copepods and Crustaceans were removed from the filter pads with very fine forceps. Prefiltration to remove these animals was not used because of the risk of losing much of the filamentous and 'colonial' forms of phytoplankton. The residues, with the exception of those used in pigment analyses, were dried to 40°C and stored in dessicators until treatment. Residues for pigment analyses were stored in a 'deep freeze' for periods up to 12 hours only before extraction.

### Dry Weight

Residues from 0.1 to 2 litres of sample were collected on pretreated (see page 16) and preweighed glass fibre papers. These were dried at 40°C for at least 24 hours and until constant weight was attained.

#### Ash-free Dry Weight

Residues used in the dry weight determination were ashed at 500°C for at least one hour and then cooled in dessicators before the remaining residue was reweighed. It was assumed that total combustion of the organic carbonaceous matter occurred and so the loss in weight of the residue was a direct measure of its organic content. The remaining residue was considered to be purely inorganic material and to give, at least in part, a crude indication of the 'silt' content of the seston. During periods of large growths of plankton, especially diatoms in the phytoplankton, this ash content would not indicate the true quantity of silt in the seston although it might well be considered as an estimate of the potential material source for silt.

#### Oxidizable Carbon Content

The particulate carbon content was estimated by wet oxidation of the residue with an acid dichromate mixture and then back titration to determine the excess dichromate not used in the reaction. The method used during this study was based on procedures previously described in A.P.H.A. (1955) and by Strickland and Parsons (1960) but it incorporates several modifications not already stated.

Dried residues from 0.1 to 1 litre of sample on pretreated filter pads were put in 100ml capacity conical flasks. The following reagents were added to each flask in rapid succession:-

glass distilled water, 0.25 N. Potassium dichromate and concentrated Sulphuric acid (s.g. 1.84) in the ratio 1:1:5. The mixture was thoroughly stirred and then the flasks and contents were heated in an oven at 100-105°C for 45-60 minutes. In this way even heating occurred throughout the reaction and to reduce contamination the flasks were loosely covered with aluminium foil caps.

At the end of the reaction period, 30ml of glass distilled water were added to each flask and the contents cooled before the excess Potassium dichromate was determined with standardised Ferrous ammonium sulphate approximately 0.025 N. with ferroin as indicator. The oxidation value from this titration was expressed in glucose - carbon equivalents. Corrections were applied for the 'bleaching' of the dichromate by the acid and the oxidant consumed by the filter pad. The correction factors for the latter were not constant and filter pad blanks were determined for every set of analyses. It was assumed that the corrected oxidation value represented the total oxidation of organic carbon compounds only and was therefore a measure of the particulate carbon. Steele and Baird (1961, 1962 and 1965) used wet oxidation to estimate the particulate carbon content of the seston in the North Sea and Strickland and Parsons (1960) considered this measure to be within 10 - 20% of the true carbon content and a realistic estimate of the energy stored within the standing crop.

### Algal Pigments

During April 1967, preliminary determinations of the 'chlorophyll a' content of the seston were made from methanol extractions. The residues were kept in the refrigerator in darkness at 0°C for 12 hours and then extracted for another 24 hours under the same conditions. A small quantity of magnesium carbonate was added with the methanol in order to reduce or retard phaeophytin production. The optical densities of the resulting solutions at 665m $\mu$ , 450m $\mu$  and 440m $\mu$  were measured on a Unicam SP500 prism spectrophotometer with a slit width of 0.04-0.06 $\mu$  and using one cm cells. A turbidity correction from measurements at 750m $\mu$  were applied to all results (Strickland and Parsons 1960). The 'chlorophyll a' content of the residue was estimated from the equation derived by Talling and Driver (1963).  
Chlorophyll a/residue = 13.9 O.D. 665

In May 1967, the extractant was changed to a mixture of solvents - methanol, ethanol, Acetone, ether and petroleum ether - in equal proportions. The procedure of prefreezing the residues before extraction was continued and the period of extraction was also kept at 24 hours, although there was evidence that it could be completed in a much shorter time. Following extraction, the residue was removed by filtration and the mixed solvent filtrate

was reduced to dryness and the total pigments redissolved in methanol. The evaporation was carried out at 30°C under vacuum and in the dark to minimise any losses due to volatilization and 'bleaching'.

In estimating the chlorophyll a content of the seston, there was no provision made to determine what percentage of this pigment was, in fact, present as magnesium-void decomposition product in the original sample and therefore the estimated 'chlorophyll a' is a measure of both. Although this could lead to serious errors in predicting the gross photosynthetic potential of populations in productivity studies (see Yentsch 1965), it is probably acceptable as a measure of biomass ~~(seston)~~ for comparative purposes since in most conditions the decomposition products will have been derived from the same population. The conditions under which these products were possibly associated with detrital organic matter and not the standing crop population usually occurred in the reservoir when the standing crop biomass was small and the measurements of pigments less reliable anyway (see section on T.P.V.).

Since it was not possible to make routine measurements of the changes in other individual pigments, especially the more commonly occurring carotenoids, the ratio of the absorbancies at 450mμ and 665mμ was determined on the methanol extract at the same time as the chlorophyll a content. This ratio was assumed to give an approximate ratio between the total 'carotenoids + products' and



the total 'chlorophylls + products' and as such to give a very approximate indication of the changes in the carotenoid pigments of the standing crop.

The change from methanol to a mixed solvent as the extractant was based on preliminary experiments with unialgal and mixed cultures which indicated that, at least, in some algae, methanol was an inefficient extractant compared with the mixed solvent.

#### Determination of Total Particulate Volume, with a Coulter Counter

Samples were stored in a refrigerator until they were analysed. If the storage period exceeded 2-4 hours, membrane-filtered formalin was added as a further preservative - 1ml of formalin (40%) to every 100ml of sample. The results of preliminary observations on the storage of samples ~~are~~ given in Table indicate that, although refrigeration was sufficient, formalin could be used instead as a form of preservative for up to seven days.

The total particulate volume of the seston was measured with an Industrial Model A Coulter Counter with a 200  $\mu\text{m}$  aperture tube. The machine was calibrated with Lycopodium spores (mean spore diameter 28 $\mu$ ) suspended in membrane-filtered 0.5% saline solution. It was decided that this was the best electrolyte and concentration which would be effective without serious changes in the phytoplankton. Later observations during the routine determination of T.P.V. showed that many species were capable of survival and even limited growth in cultures enriched with such a saline concentration. Since preliminary observations on calibration suggested that it varied slightly with the temperature of the electrolyte, the temperature was arbitrarily fixed at 20°C, and all samples were adjusted to this before the analysis was started. For routine sample analysis, a range of 12 volume intervals from approximately 35-22,000  $\mu\text{m}^3$  were used - corresponding to spherical particle diameters of 1, 2, 4, 8, 10, 12, 15, 18, 20, 30, 40 and 50  $\mu\text{m}$ . This volume range was thought to correspond closely to that of the seston trapped on the glass-fibre filters, so that direct comparisons were possible not only from week to week, but also between T.P.V. determinations, and other parameters of the seston measured at the same time.

For certain filamentous and 'colonial' forms of algae e.g. Tribonema spp., Fragilaria crotonensis and Anabaena circinalis, it was necessary to separate the cells in order to reduce size of the

'aggregates' to units sized within the range of the analysis. Pretreatment of the samples in a 'Maxomatic' ultra sonic device and occasionally with the addition of digestive enzymes, e.g. snail gut cytase, was used to effect the separation. When this technique was used, it was not possible to determine the true sestonic particle count for the sample, since an over-estimate of numbers would automatically be recorded, although the overall volume of the total seston should not be affected.

In each analysis, 285-475ml of sample were used and 15-25ml of membrane-filtered 10% saline were added to give a final concentration of 0.5% saline with the minimum dilution of the sample. Usually, for each count, 0.5ml of volume of sample were analysed, but when the particle count was low, this volume was increased to 2 ml. Several counts were made for each volume interval, as suggested by Coulter Electronics Ltd. in their manual - 2-4 for a high particle count, and 4-10 for low numbers. A correction factor, also suggested in the Manual, supplied with the machine, was applied to their mean for the effect of coincidence in which 2 or more particles are registered as a single particle, since they move through the orifice simultaneously. When this factor exceeded 10% of the mean count (10,000 particles/ml for a 200  $\mu$ m aperture tube) the sample was diluted with membrane-filtered 0.5% saline, and the analysis repeated, and a further factor was used to calculate the T.P.V. in the original undiluted sample.



The total particulate volume was calculated from the following equation:-

$$\text{T.P.V.} = v_1(N_2 - N_1) + v_2(N_3 - N_2) \dots v_{n-1}(N_n - N_{n-1})$$

where  $N$  is the number of particles and  $N_1$  is the maximum number of particles recorded at the lowest setting (both corrected for coincidence);  $v$  is the volume for the interval and is estimated for a spherical particle with a diameter equivalent to the lower limit of the interval (but see also Evans and McGill, 1969 in press). The T.P.V. calculated from this equation, is likely to be an under-estimate of the true volume, but it does represent the minimum value possible. The real value will depend on the distribution of particle sizes within the intervals which cannot be precisely measured. Maloney and Donovan (1962), Cushing and Nicholson (1966) and Parsons (1965) used the mean volume for each interval in their calculations but this volume will only give a real value for T.P.V. if the particles show a Poisson distribution within the intervals.

#### The Identification and Enumeration of Phytoplankton

Samples of water for the enumeration and identification of the main species of phytoplankton were preserved as soon as possible after collection with 1ml of modified Lugol's iodine

solution for every 100ml of sample. This solution consisted of:-

- 20 grm - Potassium iodide
- 10 grm - Sublimated iodine
- 60 ml - Glacial Acetic acid
- 200 ml - Water

Enumeration of the phytoplankton species was made with a Prior inverted microscope using methods described by Lund, Kipling and LeCren (1958) and based on the Utermohl sedimentation technique. Bipartite sedimentation chambers of 1-5ml capacity (Bellinger, 1968) were used so that some concentration of the sample was possible during the sedimentation procedure to ensure that at least 50 individuals of each species counted were present. In some samples, especially those collected during the winter months, it was necessary to concentrate the phytoplankton from a larger volume of sample and then a two-step procedure was used. Up to 100ml of sample were sedimented overnight, and then the supernatant was removed, and the remainder reconcentrated in the counting chamber.

The identification of many of the species of algae was possible as the count was continued, since the design of the sedimentation chamber was such that a high power objective could be used with optically satisfactory illumination. Usually most of the smaller species and those occurring only infrequently were

identified in this way but occasionally concentrates of the living material were made, by centrifugation of the raw water samples, and used for their identification. Many of the larger species of algae were identified in the living condition from weekly net hauls which were collected at the same time as the samples.

Diatom species were identified from frustule characteristics either by incinerating the diatom on a slide and in situ, or when a larger quantity of diatoms were available, by cleaning the frustules with hot acid.

Usually only a single count was made for each sample, and the results were expressed in cells or coenobia/ml. No attempt was made to separate the 'colonial' and filamentous forms into single cells, but when there was only a few organisms present total cell counts were made. However when those forms were present in large quantities, estimates of the total cell counts were made by multiplying the organism count by a mean cells/organism factor derived from several (10-20) random counts on the organisms. Cell counts were converted into total algal volume, so that direct comparisons were possible between standing crops of different algal composition. The cell volumes were calculated on the basis of simple geometric shapes from cell measurements of the living material.

### Physical Conditions of the Environment

The temperature of the reservoir was determined manually with a simple mercury-in-glass thermometer as the samples were collected: but more accurate measurements were available during the spring and summer months from continuous automatic recorders situated on the towers in the reservoir.

Daily variations in water level and water transparency (using a Secchi disc) were measured at the end of the outlet pier by the staff of the Metropolitan Water Board and the results were available for this investigation. Light attenuation in the reservoir was measured on several occasions with balanced selenium photocells with an instrument made in the Botany Department of Royal Holloway College and based on a design by Atkins (1923), but see Bellinger (1968).

### Regional Meteorological Information

Data for rainfall, daily rates of evaporation and total solar radiation were taken from the records supplied by the Meteorological Observatory at Kew for the region.

### Methods for Culturing Algae in the Laboratory

All pyrex glassware used in the preparation of stock media, as well as experimental work, was precleaned in chromic-sulphuric acid, and then thoroughly rinsed with distilled water (at least 10 washings) and finally with glass distilled water (at least 2 washings).

The media for both stock and experimental cultures were prepared as far as possible, from Analar-grade, reagents, and sterilized by autoclaving at 15 lbs/sq. inch pressure for 20 minutes. The sterilized media was allowed to stand for 24 hours before use.

Non-axenic stock cultures of algae isolated from both reservoir and river waters, were maintained - with fortnightly sub-culturing - in liquid non-aerated and non-agitated medium. A variety of media were used including:

- (1) Filtered river or reservoir water plus soil extract.
- (2) As (1) but with added S, P or N.
- (3) Chu 10 (Chu 1942) plus soil extract.
- (4) Rodhe VIII plus soil extract (Rodhe 1948).
- (5) A modified Rodhe VIII plus soil extract.

The Rodhe VIII medium in (5) was modified by the replacement of the iron source - iron citrate/citric acid - by a chelated mixture of trace elements (TM2 of Droop, see 1954). The media used in experimental work have been described in the section for experiments (see page 11).





Pretreatment of samples before analysis

Combined depth Sample 3.6 litres

1. Identification and enumeration of the phytoplankton. 100 ml.
2. Determination of Total Particulate Volume, 300-500 ml.  
with the Coulter Counter.

Pretreated glass fibre filter pads  
(WHATMAN GF/C.)

Filtrate

Dissolved nutrients

400-600 ml

Nitrate-nitrogen

Nitrite-nitrogen

Ammonium-nitrogen

Phosphate-phosphorus

Silicon dioxide (silica)

Residue

Glass fibre pad 1. Dry weight

and/or Organic  
matter and carbon  
100 ml - 2 litres

Glass fibre pad 2. Carbon content (wet oxidation)

100 ml-500 ml

Glass fibre pad 3. Pigment content

1-5 litres

Chapter III  
The Physical and Chemical Environment

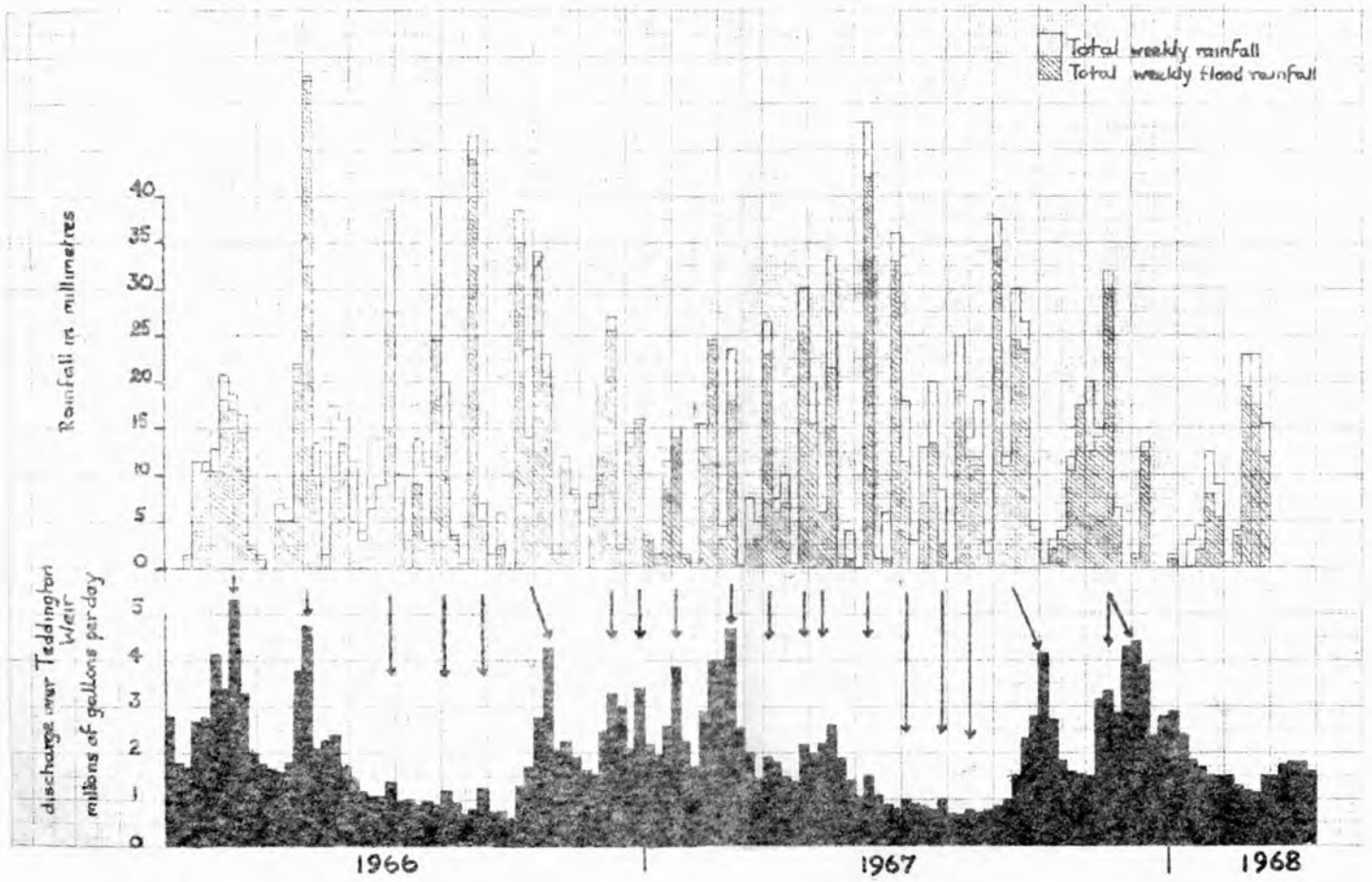
Rainfall and the Rate of Flow of the River Thames

Daily records of rainfall and evaporation losses, for South West area of London from January 1966 to the end of May 1968 were obtained from the Meteorological Observatory at Kew. Flood rainfall levels (which were assumed to indicate that amount of rain of the total fall available as run-off into the river) were determined by subtracting the daily loss due to evaporation from the total daily rainfall and the seasonal variations in both the total weekly rainfall and the total weekly flood rainfall are given in figure 2. The highest flood rainfall levels were recorded in April and August during 1966 and in June for 1967, so that there was not an obvious correlation with seasons.

There was, however, a marked seasonal fluctuation in the weekly mean flow of the River Thames, with highest flows during the winter and early spring periods and minimal flows during the late summer period. Daily records of the natural flow of the River Thames (i.e. the observed flow plus the quantity abstracted for commercial purposes) over the weir at Teddington were supplied by the Thames Conservancy Board. From these records, the weekly means were estimated and the seasonal fluctuations in the means for the period January 1966 until May 1968 are also shown in figure 2.


Fig. 2. The variation in the weekly mean rainfall, flood  
rainfall and river flow from 1966 - 1968.

FIG 2



Although there is a close correlation between the total weekly flood rainfall and the mean river flow, it is not immediately apparent from figure 2. The quantity of water in the river at any one time will depend on the balance between the replenishment from run-off and the losses to the atmosphere through evaporation. The quantity of river water flowing over the weir at any one time will depend both on the balance in the immediate vicinity of the weir (the area for which the rainfall data is available), and the balance for the region upstream to the headwaters (for which there is no data). Although flood rainfall indicates the total potential run-off, the percentage of this water which reaches the river will depend both on the rate of loss to the atmosphere by evaporation and the loss due to the 'terrestrial requirement' (mainly through vegetation). Thus during the winter periods (including early spring) when this percentage is high, since there are only small losses, high flows are recorded, with obvious fluctuations, associated with small changes in flood rainfall. An increase in vegetational cover and the rate of evaporation to the atmosphere as the summer progresses results in a corresponding decrease in the availability of the flood rainfall as run-off, which coupled with the evaporation losses of the river water must account for the continually low summer flows, with only small fluctuations, for even very large variations in the recorded flood rainfall.

An obvious correlation was not found between the total seston in suspension in the river (as determined as T.P.V.) and the





weekly mean flow, although high levels of chlorophyll in the seston (indicating large crops of phytoplankton) were always associated with low flows. This is in accordance with results for the River Lee from which Swale (1964) suggested that large standing crops of phytoplankton and thus plankton production occurred during periods of low rates of flow. The effect of river flow on the chemistry of the water, and thus indirectly on that of the reservoir water, is discussed in section III on chemistry.

#### Water Level in the Reservoir

Since the inflow of river water into Thames Valley reservoirs is controlled by the Metropolitan Water Board, the rate of flow in the River Thames can only have an indirect influence on the physical conditions in the Q.E.II reservoir, by virtue of its effect on the suspended seston load and possibly the temperature of the inflowing water. The rate would not have any influence on the total volume of water in the reservoir and thus, at complete variance with what might be expected in natural bodies of water, there was an ~~association~~ association between high rates of flow in the river and reduced water levels (and hence reduced water volume) in the reservoir. In accordance with Metropolitan Water Board policy, the water levels were reduced during the winter and early spring periods and then raised in the early summer and maintained throughout the summer, as far as possible, at the top water level (T.W.L.) indicating full use of storage capacity.

During the winter 1965-1966, the minimum water level was recorded at 4 feet and 2 inches (approximately 1.3m) below T.W.L. on 10.1.66. The level was then gradually raised and T.W.L. was reached at the beginning of April and then maintained at T.W.L. + 4 inches throughout the summer. Reduction of the level for the winter period 1966-1967 was started in mid-October and then kept between 17 and 24 inches below T.W.L. The 1967 summer level of T.W.L. + 7 inches was not attained until mid-June which was some 2 months later than in 1966. This was probably due, in part, to the increased water throughput in spring 1967 compared with the same period in 1966. Similarly, the rate of throughput was probably responsible for the sudden drop in mid-August although the winter lowering was not started until mid-October. By the end of November 1967 the water level was at 80 inches below T.W.L. and this low level was maintained between 60 and 70 inches below T.W.L. until the end of January. During February 1968 there was a slight increase in the water level but this was then lowered again in March 1968 and a winter minimum was recorded at the end of this month at 84 inches below T.W.L. By the end of May top water level had still not been reached.

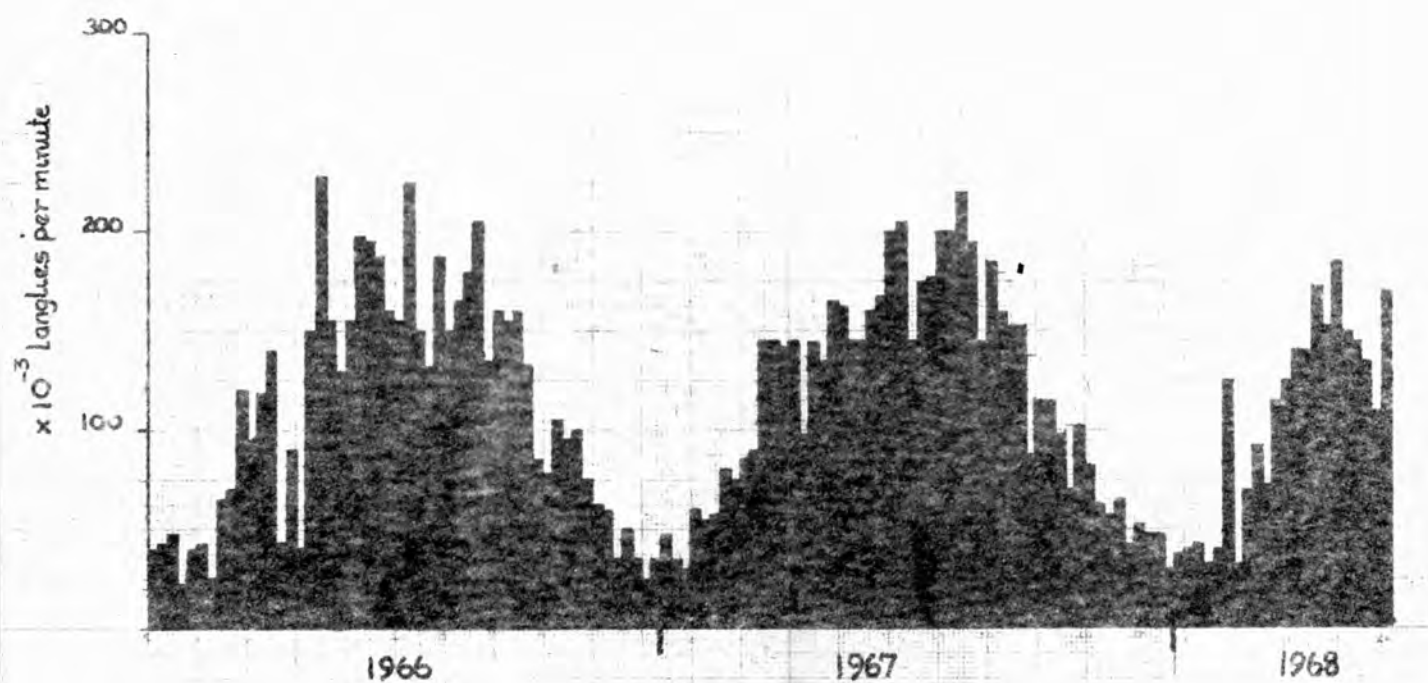
### Solar Radiation, Water Transparency and Light Attenuation

Daily records of the total solar radiation, expressed in milliwatt hours/cm<sup>2</sup>, were obtained from the Meteorological Office at Kew Observatory. Weekly means of these figures, for the period January 1966 until May 1968, were converted into langlies/minute and corrected to give weekly mean estimates of the incident effective energy for photosynthesis. It was assumed that this energy ranged from 3800Å - 7200Å in wavelength and accounted for half the total incident radiation (see Strickland 1958). The seasonal variation in this radiant energy is given in figure 3 . Even during the winter periods, when the records for the weekly means were at their lowest values, they were still an order of magnitude greater than the values of the compensation energy (defined as the level of energy at which gross photosynthesis is balanced by losses due to respiration so that there is no net production), reported by various workers in both marine and freshwater plankton (see Strickland 1960).

However, it seems very likely that radiation during the winter and early spring months was a major factor in the limitation of plankton production in the reservoir. For although the surface energy was sufficient, there would be a marked reduction in the intensity as the energy penetrated through the water to an intensity approaching, or perhaps lower than, the compensation value. Thus under the turbulent water conditions that occur in the reservoir, and the reduced daylength of winter, it is probable that the plankton population would barely fix enough carbon to survive and rarely enough to increase.

Fig. 3. The photosynthetic radiation incident on the water surface of the Queen Elizabeth II reservoir - each plot represents the weekly mean.

FIG. 3





The penetration of light in the reservoir was measured on three occasions during the course of this study, with a submersible light meter (see page 32). Each time, the measurements were made at approximately mid-day when conditions in the reservoir were calm and there was little or no cloud cover.

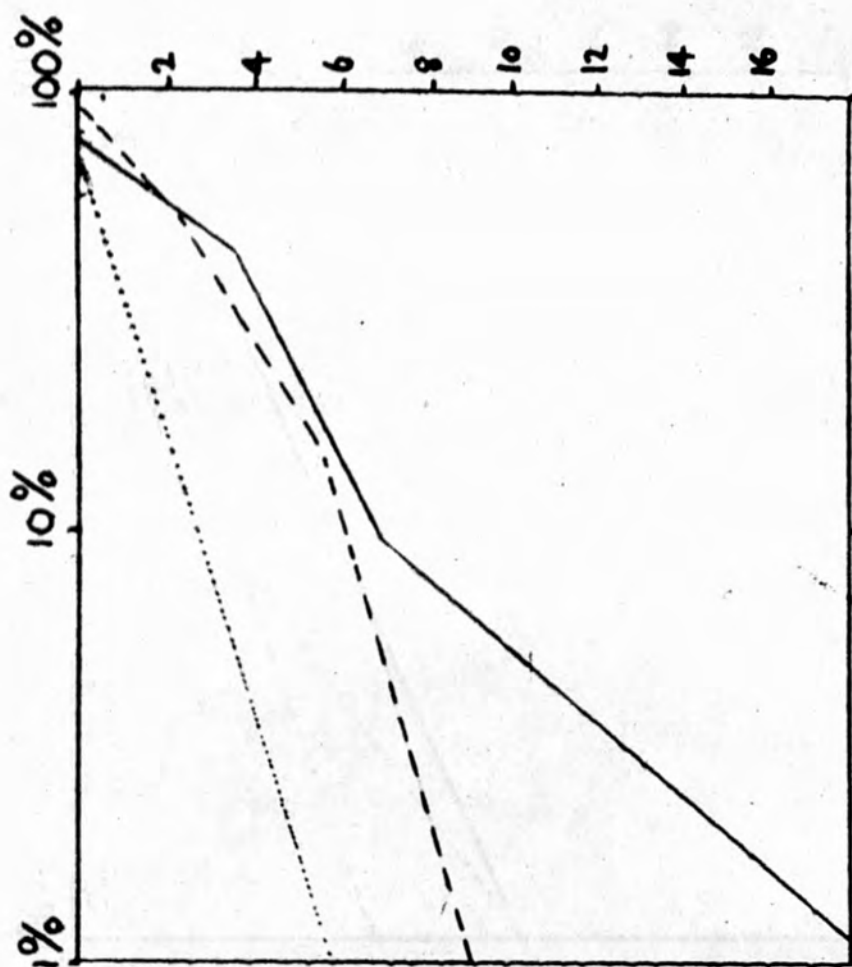
In April 1967, August 1967 and March 1968, the penetration of the red, green and blue components of light were measured, but only in April 1967 and March 1968, was the total light attenuation measured. Also in April 1967, the yellow component of the light was measured through the depths of the reservoir, but its measurement was omitted on the other two occasions.

Since both the quantity and the quality of the total matter in suspension can have a profound effect on light attenuation the results, shown as figure 4, were plotted in semi-logarithmic form so that a direct comparison could be made between each light gradient and the vertical distribution of the seston in suspension in the reservoir at that time (determined as T.P.V.). It was not unexpected that the peak transmission was in a different range of the spectrum on each of the occasions.

In April 1967, the high T.P.V. levels indicating marked turbidity were for the most part due to large numbers of diatoms ~~(*Chaetoceros*)~~ in the seston, and the most penetrating component of the sub-aquatic light was the red part of the spectrum and the least penetrating the blue. Similarly, in March 1968, when the water was similarly turbid (the values of T.P.V. being lower than in April

Fig. 4. The penetration of light (expressed as percentage transmission) compared with the variation in particulate seston (expressed as volume in  $\text{mm}^3/\text{L}$ ) in the Queen Elizabeth II reservoir, on three occasions in April 1967, August 1967 and March 1968.

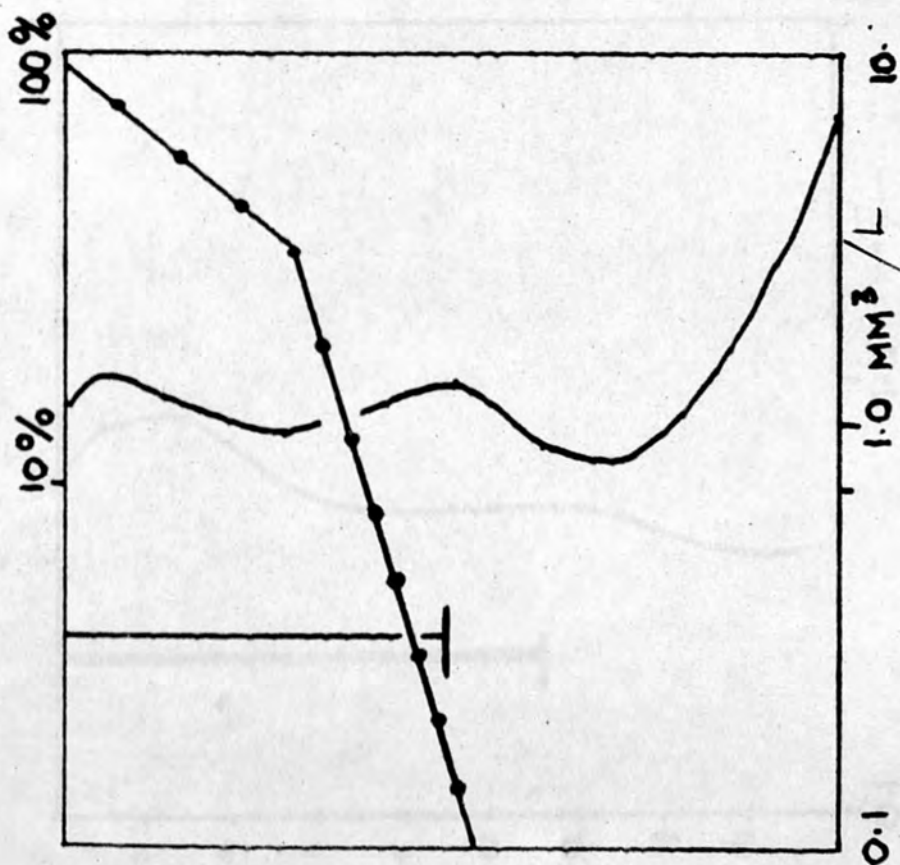
MARCH 1968



..... BLUE LIGHT

----- RED LIGHT

—— GREEN LIGHT.



└ SECCHI DISC DEPTH

—•— TOTAL LIGHT

—— T.P.V. ( $\text{mm}^3$  per litre)

FIG. 4.

FIG. 4 [CONT'D.]

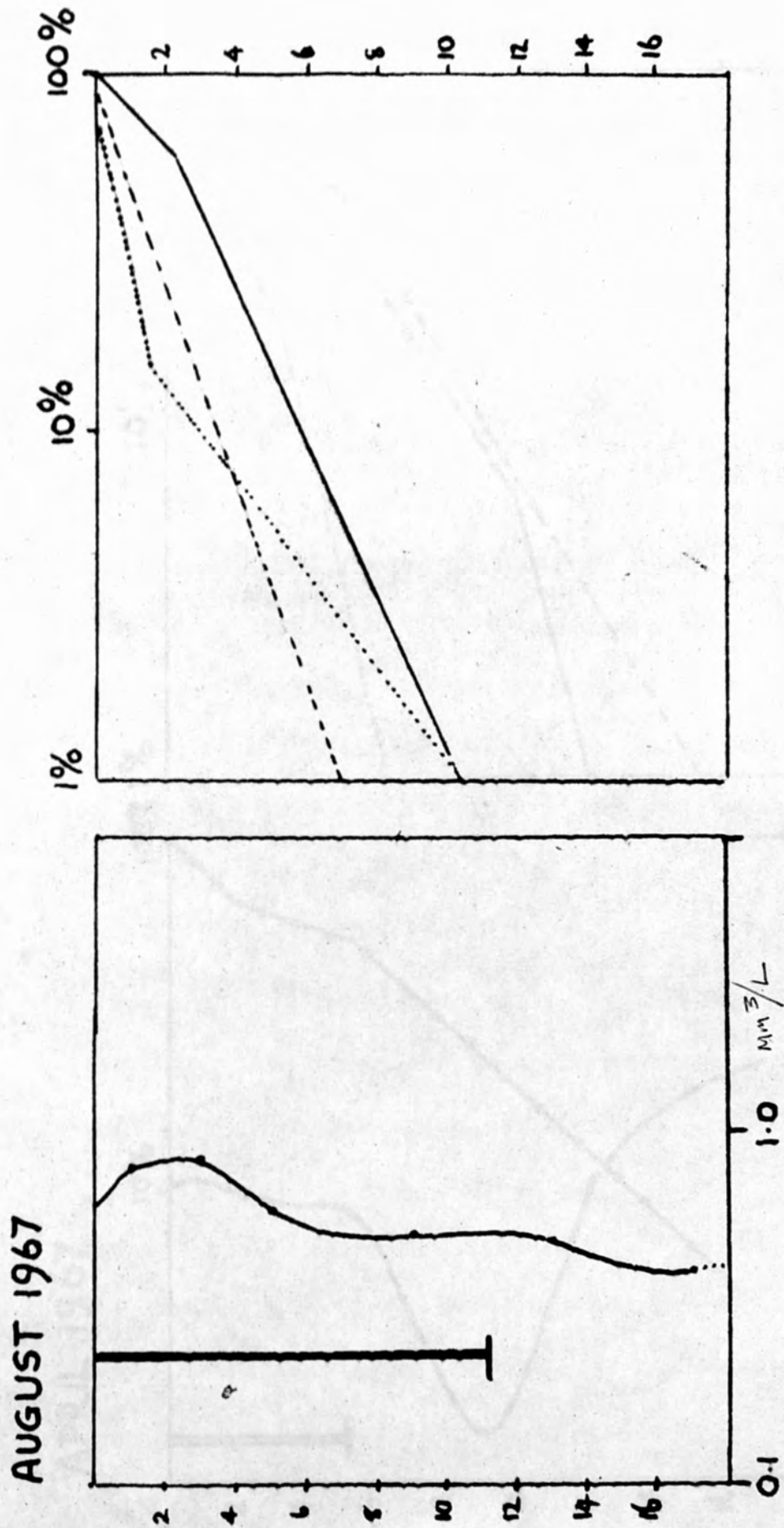
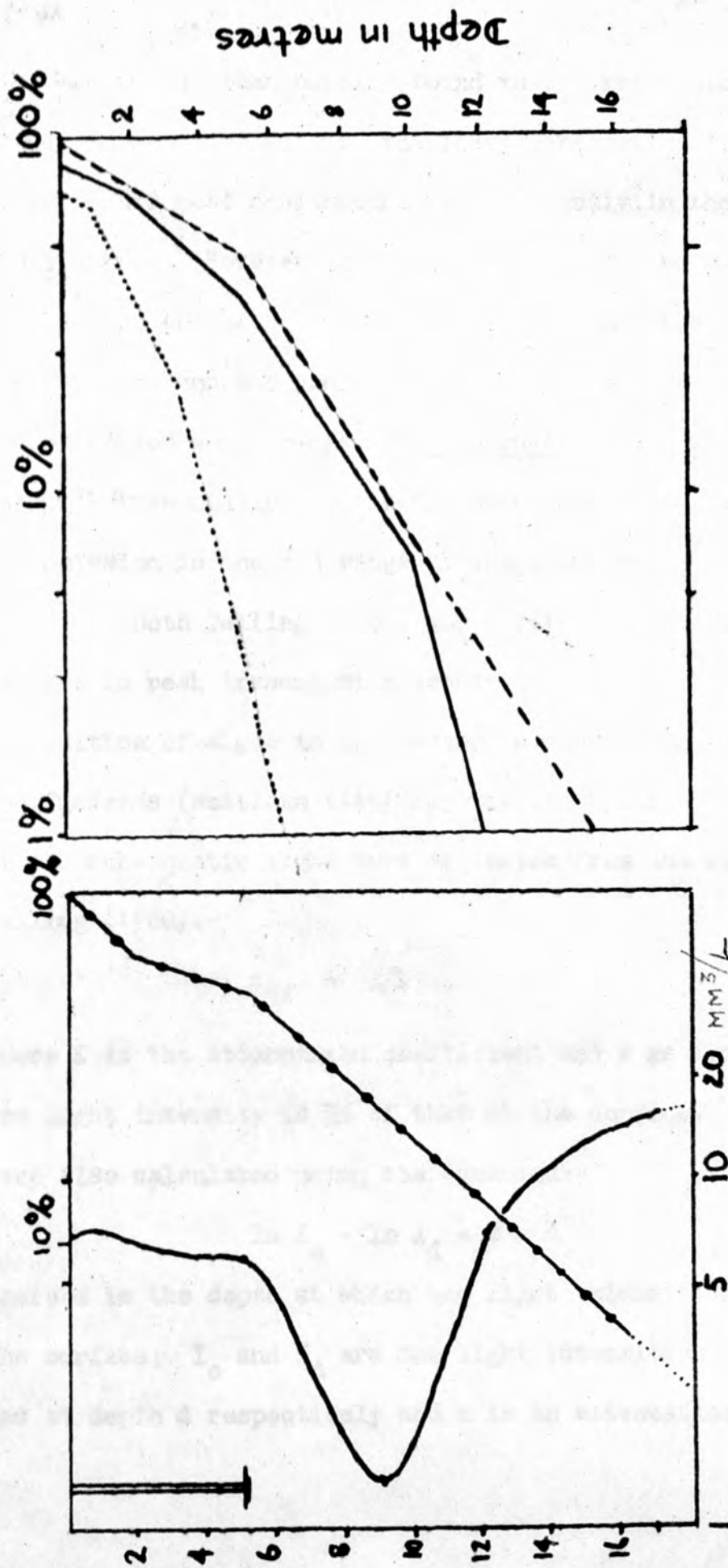


FIG. 4 [CONT'D.]

APRIL 1967





1967 but higher than usually found in the reservoir) but the seston composed mainly of debris, the least penetrating component was blue although the most penetrating was apparently in the green region of the spectrum. However, in August 1967, when the water was less turbid than on the other two occasions (since the T.P.V. throughout the water column was considerably lower) and the dominant phytoplankton were species of Tribonema and Anabaena (see page ) the peak transmission was in the blue region and the minimum transmission in the red range of the spectrum.

Both Talling (1960) and Bellinger (1968) have reported changes in peak transmission associated with differences in the composition of algae in the seston in suspension. Attenuation coefficients (Westlake 1965) for the total light and each component of the sub-aquatic light were estimated from the equation derived by Talling (1960),

$$z_{5\%} = 3/K$$

where K is the attenuation coefficient and z is the depth at which the light intensity is 5% of that at the surface. These coefficients were also calculated using the equation:-

$$\ln I_0 - \ln I_d = k \times d$$

where d is the depth at which the light intensity is 1% of that at the surface;  $I_0$  and  $I_d$  are the light intensities at the surface and at depth d respectively and k is an attenuation coefficient.

The difference in the values of the corresponding coefficients calculated by the two methods is considered to be a reflection of the influence of suspended seston (in this case in the lower depths of the reservoir) on light attenuation (see Table 1). The values obtained by the Talling equation were used in further calculations on light penetration (see section on light availability page 49). Although light attenuation was measured only on these three occasions daily variations in water transparency, as measured by Secchi disc depth readings, were available for the whole of the period of the investigation from the Metropolitan Water Board. The maximum reading of the Secchi disc depth was limited to 13 feet (approximately 4.3m) so that transparencies greater than this depth were recorded as 13 feet<sup>+</sup> and direct comparison between these depths and transparencies less than 13 feet were not possible, since the variation from day to day was not known. Strickland (1958) suggests that in the top 2.5 - 25 metres of water, secchi disc measurements may be used to give a very approximate idea of attenuation coefficients, and the range of values for the coefficient (for total light) was calculated from his modification of the equation derived by Jones and Wills (1956). This range was between 0.208 and 0.676 and compared fairly well with the values derived by measurements with the light meter (see page 40).

There have been many reports in the literature for both marine and freshwater habitats of the relationship between secchi disc

Table 1

Comparison of light attenuation coefficients for  
red, blue, and green lights and total light

April 1967

	Total	Red	Green	Blue
Attenuation coefficient				
K (using equation 2)	0.209	0.302	0.370	0.685
K (secchi disc depth)	0.348			
K (Talling's equation)	0.181	0.273	0.268	0.6

August 1967

	Total	Red	Green	Blue
Attenuation coefficient				
K (using equation 2)		0.850	0.441	0.396
K (secchi disc depth)	0.232			
K (Talling's equation)		0.628	0.476	0.417

March 1968

	Total	Red	Green	Blue
Attenuation coefficient				
K (using equation 2)	0.460	0.501	0.234	0.74
K (secchi disc depth)	0.348			
K (Talling's equation)	0.385	0.424	0.256	0.77

readings and the depth of the euphotic zone (defined at its lower limit as the depth at which the light intensity is reduced to 1% of the surface value), although there is considerable range of values quoted for a conversion factor (see Strickland 1958 for references). Using a value of 3 (Riley 1941) as the conversion factor, the depth of the euphotic zone in the reservoir for the period January 1966 until May 1968 was estimated and the results were compared with the compensation depth calculated for the same period shown in figure . ? The estimated depth of the zone compared closely with the upper limit of the calculated compensation depth for most of the period, except when there were marked increases in the seston in suspension (as indicated by vertical arrows in Figure 6) and thus in turbidity which was not allowed for in the calculation of the compensation depth (see section on light availability for further discussion).

#### Thermal Conditions in the Reservoir

From the data collected during the weekly sampling routine, and from the automatic recorders situated on the observation towers in the reservoir, the depth/time diagram of the thermal conditions in the Q.E.II reservoir during the period January 1966 until May 1968 was constructed as shown in figure 5. Isothermal conditions were recorded throughout the winter and early spring periods and although at no time was any ice cover reported, a minimum temperature of 2°C was recorded throughout the depths on 19.1.66 during the winter 1965-1966. In the winters 1966-1967 and 1967-1968, the recorded temperature in the reservoir did not fall below 4°C. Thermal

Fig. 5. Depth - time distribution of temperature in the  
Queen Elizabeth II reservoir from 1966 - 1968.



FIG. 5

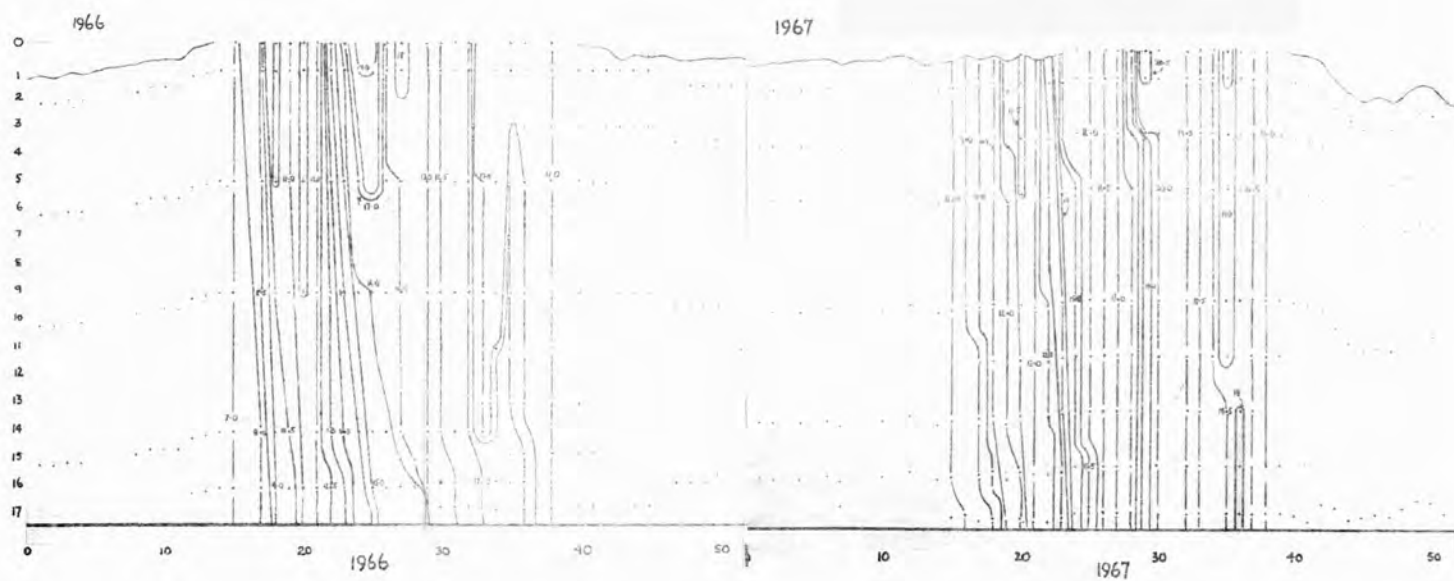
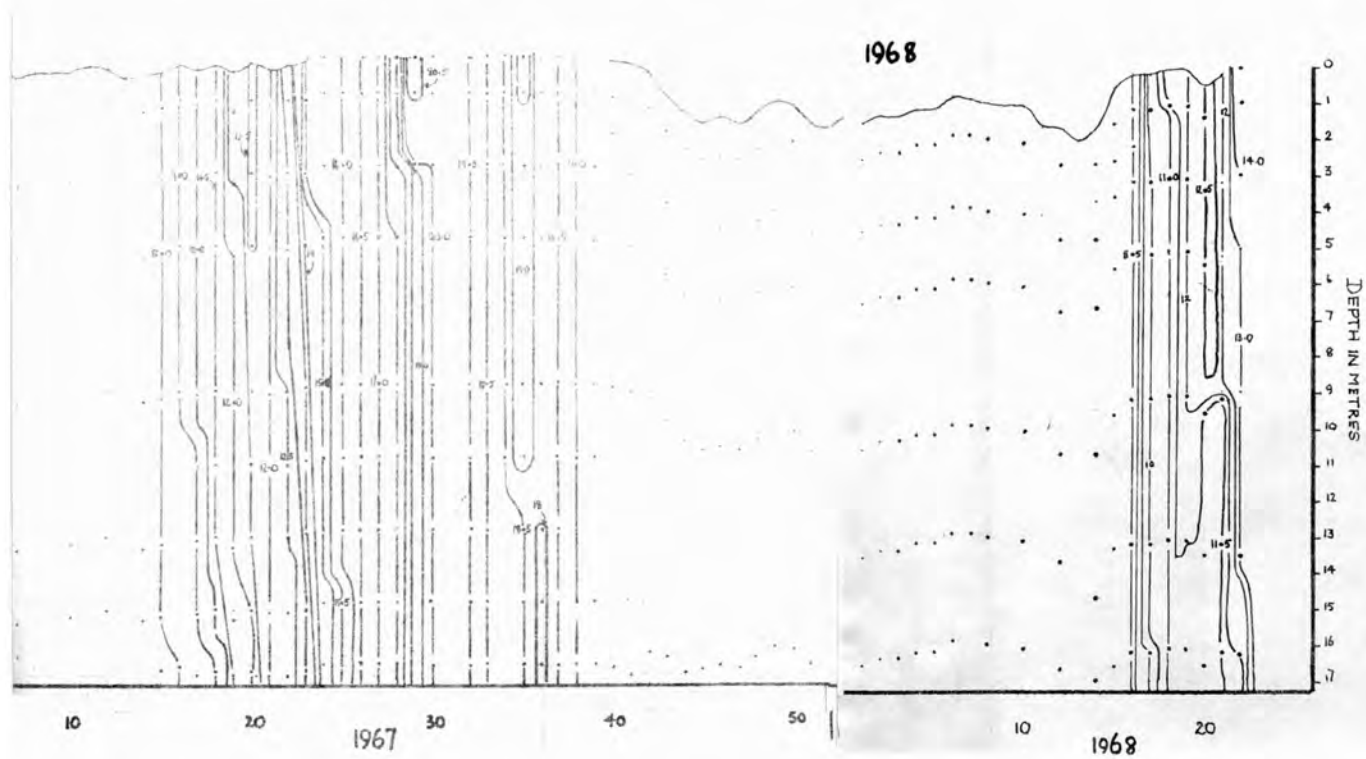


FIG. 5



discontinuities occurred in the late spring and summer during each year but throughout the period of this study, there was apparently insufficient water stability to allow the development of a marked thermal gradient with a true thermocline (defined as the stratum of water in which the thermal conditions are such that there is a change of at least  $1^{\circ}\text{C}$  per metre in depth in the thermal gradient). This observed thermal regime in the reservoir is very different from that which would have been expected if only the position and the morphometry of the reservoir were considered. On these considerations the Q.E.H. reservoir should be classified as a dimictic lake with a holomictic circulation, according to Hutchinson's proposals for lake classification on their thermal regimes (see Hutchinson Volume 1, 1957) and therefore exhibit a marked summer thermal stratification. The major factor responsible for this difference must be considered to be the turbulence imposed in the reservoir by the injection and abstraction of water into and out of it and the methods by which these operations were carried out. Thus, although there was no information on turbulence from direct measurements of currents, it has been possible to interpret, at least in part, large changes in turbulence from the thermal conditions in the reservoir.

From January 1966 until May 1966, the inflow of 35 m.g.d. was through  $2 \times 22\frac{1}{2}^{\circ}$  inlet jets and although isothermal conditions were maintained for most of this period, a distinct thermal discontinuity developed in the upper layers of water at the end of April. Apparently this stratification was not very strong since by the end of May isothermy reoccurred. The change over to six jet inlets -  $3 \times 22\frac{1}{2}^{\circ} + 3 \times 45^{\circ}$  - on 24.5.66 with the same inflow as before, was thought to reduce the internal velocity of circulation by about half (see Cooley 1954) and a thermal stratification with a temperature difference between top and bottom of  $5^{\circ}\text{C}$  developed within 14 days of this change. On 6.7.66 the inlet regime was returned to the original combination of  $2 \times 22\frac{1}{2}^{\circ}$  jets so that the internal circulation velocity was increased to its former value with the result that isothermal conditions were imposed in the reservoir by 20.7.66 when there was a change in the outlet from the centre of the reservoir floor to the outlet pier about 9m below the surface. Throughout August 1966, there was a slight thermal discontinuity in the top layers of water which suggested that the inlet system and rate of throughput was insufficient to combat the natural tendency to stratify. In spite of a change in inlets to two horizontal jets on 1.9.66 and the addition of a third a few days later which would probably result in reduced vertical turbulence, isothermal conditions prevailed in September. Thus it seems most likely that the instability of the water column was partly due to the occurrence of natural destratification and overturn during this period. Isothermality was

recorded in the reservoir for the rest of the winter 1966-1967, and a change to both the Bellmouth inlets did not alter the thermal profile. Similarly the closing of these inlets on 6.2.67 and the opening of one  $22\frac{1}{2}^{\circ}$  jet and then a second on 14.3.67 with an increase in flow rate from 30 m.g.d. to 90 m.g.d. did not affect the profile. At the end of February the outlet was changed from the pier to the floor of the reservoir. By mid-April 1967 however, there was a small thermal gradient noticeable in the upper layers of water even though the flow rate was being maintained between 70 and 120 m.g.d. and this gradient persisted as the two jet inlets were closed and replaced by the two Bellmouths on 25.4.67. However one  $22\frac{1}{2}^{\circ}$  jets was reintroduced on 28.4.67 and then on 6.6.67 the two Bellmouth inlets were closed and the summer jetting regime of  $2 \times 22\frac{1}{2}^{\circ}$  plus  $1 \times 45^{\circ}$  jets was started on 15.6.67. Isothermal conditions occurred within 14 days of the introduction of this system so that it was apparent that there was sufficient expendable energy to promote isothermy even though the internal circulation velocity may well have been reduced. Slight thermal discontinuities were recorded in early July and later in early September but since there was isothermality throughout August, these gradients were probably due to superficial heating and changes in turbulence. In early November, one of the  $22\frac{1}{2}$  jets was replaced by the two Bellmouths and then a further jet ( $45^{\circ}$ ) was also closed. These changes produced no effect on the temperature profile and it is most probable that destratification by natural means would have taken place at a much earlier date. In December 1967 all the jet inlets were opened



and the rate of flow was reduced to approximately 50 m.g.d. On 1.1.68 all the inlets except the two Bellmouths were closed and the flow was maintained at about 70 m.g.d. At the beginning of April 1968, one of the Bellmouth inlets was replaced by a  $22\frac{1}{2}^{\circ}$  jet and then another jet was also added and the flow rate was increased to 80 - 127 m.g.d., but by the end of this month there was a slight thermal gradient. This persisted for the rest of May when the Bellmouths were closed and then replaced by  $22\frac{1}{2}^{\circ}$  jets and there was a temperature difference between top and bottom of  $3^{\circ}\text{C}$ . It would appear from this gradient, that there was not sufficient energy within the jetting inlet regime, although the flow rate was high, to keep the reservoir in full circulation. The natural turbulence in the Q.E.II reservoir is supplemented by the circulation induced by the enforced, but controlled, throughput of water. This control is effected by alterations to the inlet/inflow and outlet/outflow systems and their positions relative to each other. Alteration to the systems was made by changing either the type and/or number of inlets (or outlets) or the quantity and rate of inflowing (or outflowing) water or all three factors. The magnitude of the imposed turbulence depends not only on these alterations, in particular those to the inlet/inflow system, but also on the extent of the natural stability of the water column. The relative effect of these factors was estimated, by assigning to each an arbitrary

scale of the degree of influence although, for simplicity, the effect of the outlet/outflow system on the turbulence was deliberately ignored. An index of the imposed turbulence was then calculated from the equation:

$$I = (a + c - d) \div b \text{ (See Table 2)}$$

where I is the index proportional to the imposed turbulence, and a, b, c and d are the index values for the type and numbers of inlets in use, the quantity of the inflow and the tendency for natural stratification, respectively. A comparison of the variation in this index with changes in the standing crop of phytoplankton and the development of thermal gradients in the reservoir, during this investigation, is given in figure 6. With the exception of the small gradient developed during September 1967, there was a close correlation between the occurrence of thermal gradients and the reduction in the index value (indicating a decrease in the imposed turbulence). However, although it was apparent that these gradients did not develop if the index value exceeded 30, there was not a direct relationship between the index value and the extent of the gradient. Thus at the end of May 1968 a thermal gradient of 3°C difference between the surface and bottom of the reservoir was recorded and the index value was 26, but at the end of August 1966, the observed gradient was only 2°C difference whereas the index value was 15. It

Table 2

Index of Turbulence (Arbitrary Scales)

(a) <u>Type of inlet</u>	Bellmouth	Horizontal jet	22 $\frac{1}{2}$ $^{\circ}$ jet	45 $^{\circ}$ jet
Induced horizontal turbulence	1	3	2	0
Induced vertical turbulence	1	0	2	3
Total index value	2	3	4	3

(b) No. of inlets

Index value inversely proportional to the number of inlets

(c) Quantity of inflowing water

Index value  $\equiv$  mean daily flow for each week

(d) Tendency for natural stratification (based on water temperature)

<u>Week in Year</u>	<u>Temperature of Water Column</u>	<u>Index Value</u>
1 - 10 ) 48 - 52 )	0 - 5 $^{\circ}$	1
11 - 16 ) 45 - 47 )	6 - 10 $^{\circ}$	4
17 - 24 ) 41 - 44 )	11 - 15 $^{\circ}$	9
25 - 40	> 15 $^{\circ}$	16

INDEX =

$[(\text{Index for type of inlet} + \text{inflow index}) - (\text{index for natural stratification})]$

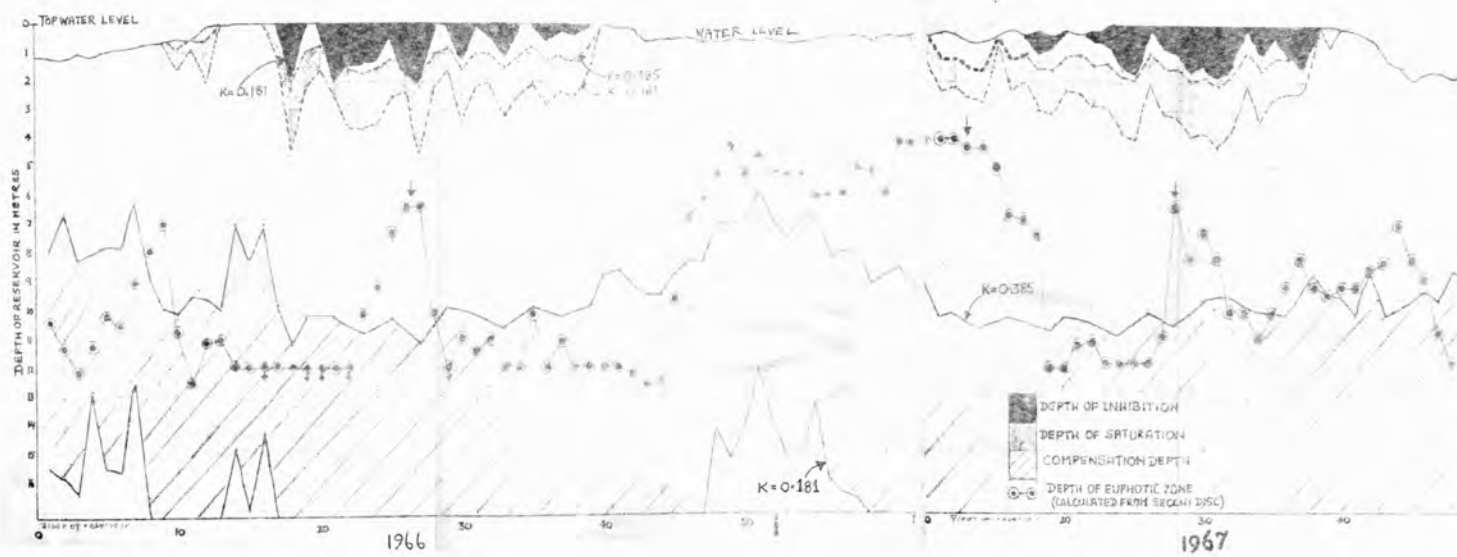
Index for no. of jets

$$= [(a + c) - d] \div b$$

Fig. 6. (a) Depths of light inhibition, light saturation, temperature and the euphotic zone in the Queen Elizabeth II reservoir during 1966 to 1968.

(b) Turbulence, thermal gradients, standing crop of phytoplankton (expressed as T.P.V. and chlorophyll 'a'), and the inflow (in millions of gallon per day) in the Queen Elizabeth II reservoir during 1966 - 1968.

Fig. 6(a)





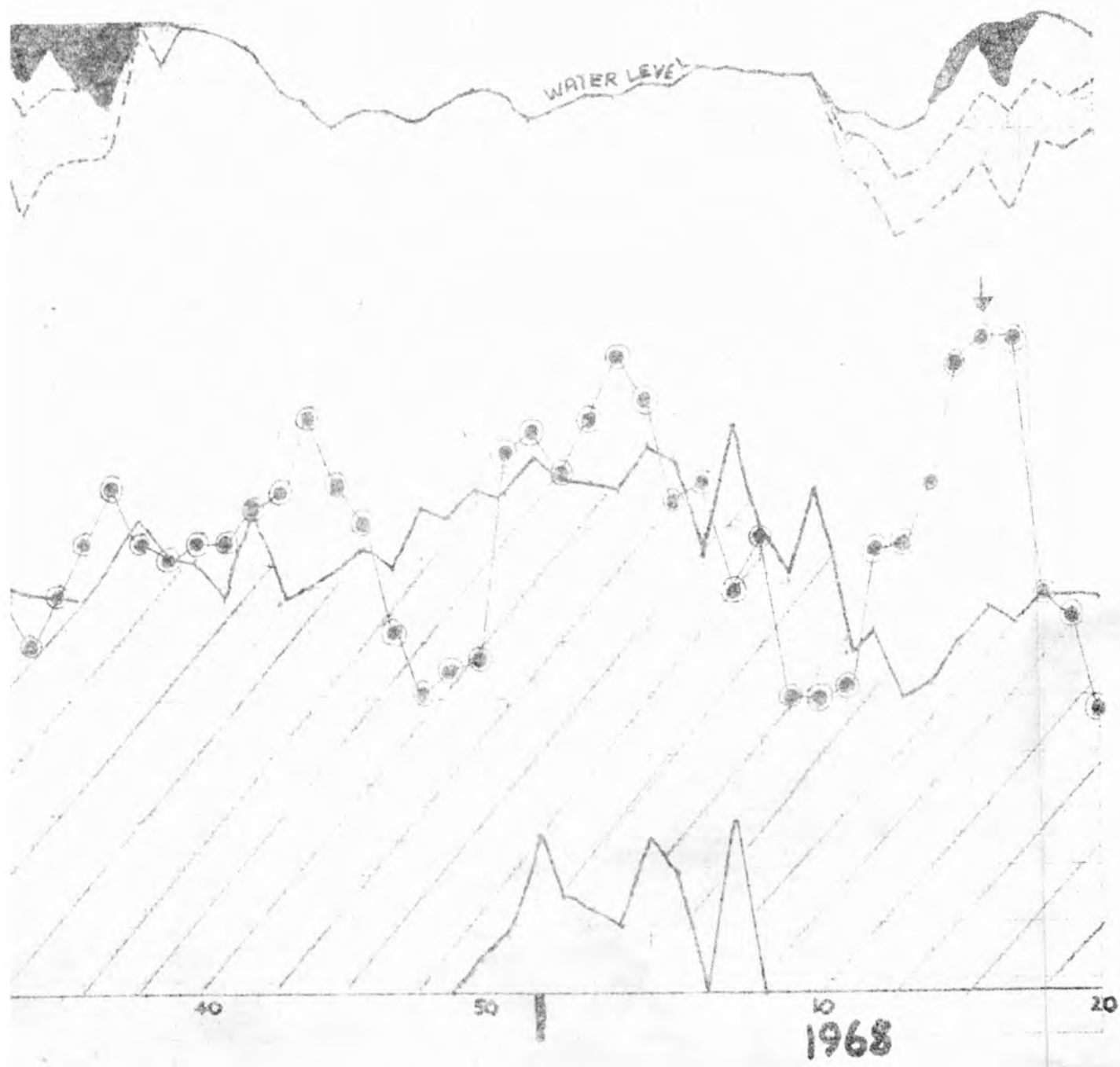
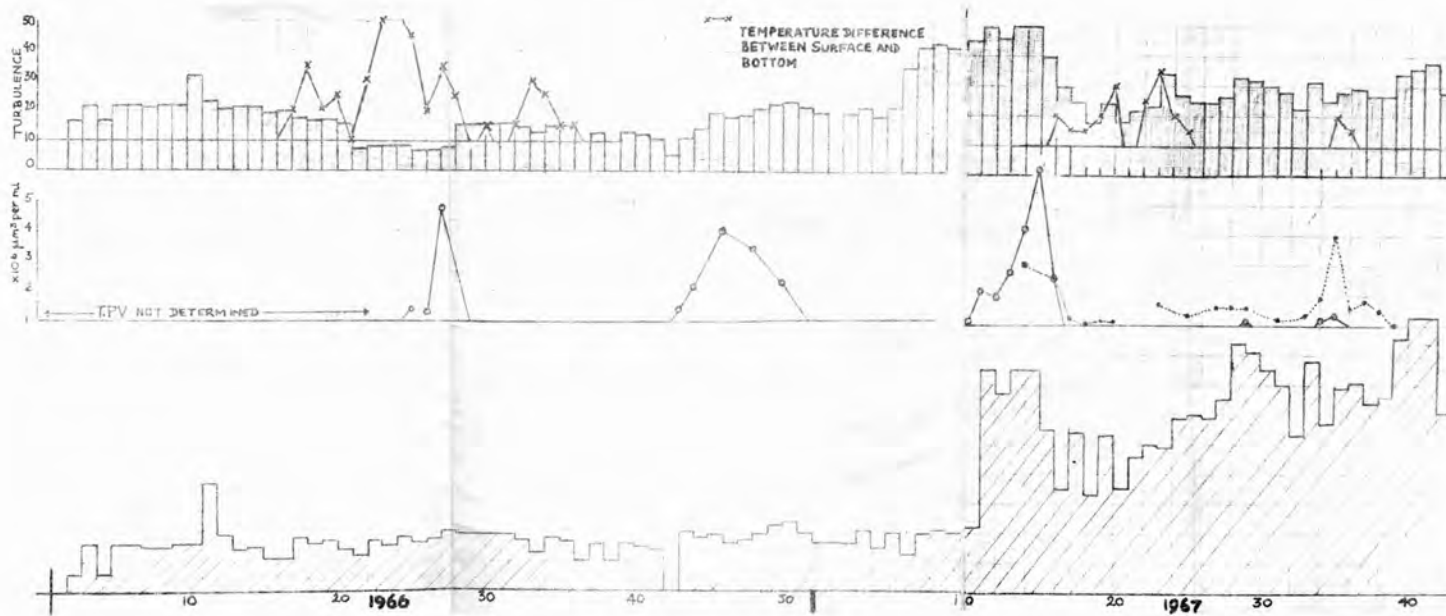
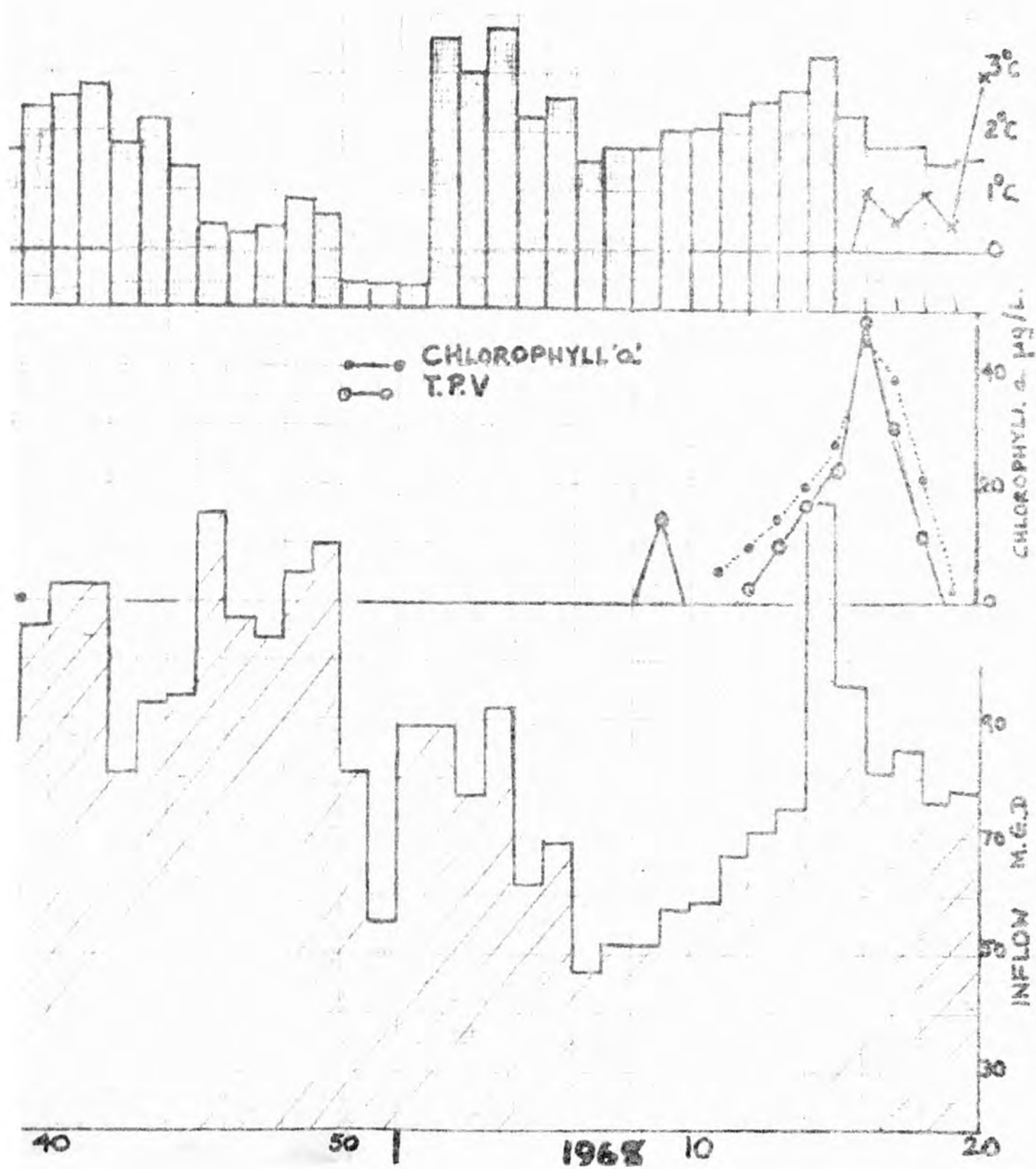


FIG. 6(b)





seems very likely that this discrepancy was due to the natural turbulence in the reservoir at these times. Since the index represents the imposed turbulence, it will only reflect the level of the 'total turbulence' in the reservoir and thus be directly related to the thermal conditions when the natural turbulence approaches zero. Such a condition was met during June and early July 1966, when weather conditions were warm, dry and calm and a thermal gradient of  $4^{\circ}\text{C}$  difference developed. The index value at this time was between 7 and 8 which probably indicated the level of the 'total' turbulence and not only the imposed turbulence.

#### Turbulence, Light Availability and Standing Crop Production

The effect of turbulence on algal production through its influence on turbidity and thus the penetration of the effective energy available for photosynthesis, and in maintaining phytoplankton in suspension, is well known and there are many cases cited in the literature to its beneficial (e.g. the effect on the growth cycle of Melosira italica; Lund 1954) and detrimental (Gran and Baarud 1935) effects.

Following the work of Gran and Baarud and later that of Riley (1941), in an attempt to formulate the relationship between these factors, Sverdrup (1953) introduced the concept of the 'compensation' and 'critical' depths. He defined the latter depth as that below which vertical mixing of the upper layers of water could not extend and still result in a net positive production of

organic matter within these layers. The compensation depth was considered to be the depth at which the light intensity was such that there was a zero net production. In deriving the equations to calculate these depths, he made the following assumptions:

- a) The plankton were homogeneously distributed in a thoroughly mixed top layer of water.
- b) That at no time was there nutrient limitation.
- c) The photosynthetically - effective energy has a range in wavelength from  $4200\text{\AA}$  to  $5600\text{\AA}$  and represents 20% of the total solar radiation.
- d) That the radiant energy at the compensation depth could be determined.
- e) That the photosynthesis at any depth was directly proportional to the light intensity at that depth.
- f) That the vertical attenuation coefficient remained constant.

The mathematical basis of Sverdrup's concept as a model for estimating plankton production has been criticised mainly on assumptions a, e and f and subsequently several attempts have been made to revise and improve the model (see Cushing 1962; Murphy 1962 and Patten 1965). However in this study, an attempt has been made to demonstrate only the relation between the incident radiation, turbulence and the observed phytoplankton production (in terms of the



standing crop) and therefore Sverdrup's model was considered to be adequate.

Sverdrup defined the compensation depth  $D$ . by:

$$D = \frac{1}{k} \log_e \frac{I_e}{I_c}$$

where  $I_e$  is the average energy penetrating the water surface,  $I_c$  is the energy at the compensation depth and  $k$  is the vertical attenuation coefficient. This equation was used to estimate the compensation depth in the reservoir and also to estimate the following depths:

- 1) Depth of inhibition which was defined as that depth to which photosynthesis is adversely affected by the light intensity.
- 2) Saturation Depth which was defined as the depth to which the rate of photosynthesis is independent of the light intensity.

The seasonal variations in these three depths for the period January 1966 until May 1968 are given in figure 6. The 'calculated critical' depth was much greater than the total depth of the reservoir throughout the period of study (a minimum value calculated during the winter season was 35 metres - twice the depth of the reservoir basin) and therefore it was concluded that at no time was the production of organic matter fully limited by the turbulent conditions. In the calculations of these depths it was necessary to make the following assumptions:

- a) The principles and experimental data for marine plankton production may be applied to plankton in freshwater situations.

- b) The effective energy for photosynthesis is between  $3800\text{\AA}$  and  $7200\text{\AA}$  in wavelength and when measured in langlies/minute is 50% of the total solar radiation.
- c) The energy at the compensation point is approximately  $3 \times 10^{-3}$  langlies/minute (ly/min): the energy at the saturation level is approximately 0.1 ly/min and that it becomes limiting through inhibition at 0.15 ly/min.
- d) The surfaces 'losses' in energy as the incident radiation penetrates the water surface were 15% of the incident total radiation.
- e) The two values for k (the vertical attenuation coefficient) used in the calculations were at the limits of the variation in this coefficient in the reservoir and thus allowed for the fact that the vertical attenuation coefficient does not remain constant (assumption e of Sverdrup on page 50).

Assumptions b, c and d were based on the references quoted in Strickland (1958) but the saturation and inhibition energies and the value for surface 'losses' were each a compromise of all the available data and therefore, as such, quite arbitrary. The validity of assumption e for the extent of the variation of the vertical attenuation coefficient in the reservoir, is in some doubt. The two values of this coefficient used in the calculation of the compensation, inhibition and saturation depths were determined from measurements of light penetration in the reservoir with a submersible light

meter (see page 40).

A comparison of these two values with the range of values for the coefficient estimated from the daily changes in the Secchi disc depth, suggested that they were not at the limits of variation for the coefficient in the reservoir. However, the higher value,  $k = 0.385$ , was close to the mean of the range and therefore it seems likely that, except for periods of low transparency, the assumption was acceptable. During these periods of low transparency the upper limit of  $k$  (0.385) was a considerable underestimate of the true value. The main discrepancies occurred during the winter period 1966-1967 and during the periods when large standing crops were observed. At these times the assumption would be incorrect, but at the initiation of the large crop increases, the limits of  $k$  and thus the assumption would still be valid. The relatively simple conditions during which an increase in a population is entirely dependent on the specific growth rate and the length of time the population is allowed to photosynthesise at the maximum rate, rarely if ever occurs in natural environments. Instead, the rate of increase is modified and ultimately governed by a variety of external environmental factors of which light, temperature and nutrient levels are probably the most important, and it is this rate which is usually observed and measured.

The observed rate of increase in standing crop is usually the integrated expression of several such rates for different populations coexisting in the environment but not necessarily at the same stage in development. As such, the rate of change in the

standing crop is a convenient assessment of the overall effect of environmental factors on phytoplankton at any particular time.

During the period of investigation from May 1966 until May 1968, large increases in standing crop, indicated by increases in T.P.V. (which were confirmed by associated increases in 'chlorophyll a' for the period May 1967 - May 1968) were only recorded on four separate occasions as shown in figure 6. These increases - for T.P.V. to a level greater than  $10^6 \mu\text{m}^3/\text{ml}$  ( $1\text{mm}^3/\text{litre}$ ) and 'chlorophyll' greater than  $10\mu\text{g}/\text{litre}$  - occurred in early summer 1966 (a population composed mainly of Tribonema spp., Fragilaria crotensis and several colonial chlorophycean species see page 133); in the early winter 1966-1967 (the population dominated by a species of Coscinodiscus see page 135) and in the spring of both 1967 and 1968 (the crop was composed of several species of diatoms see page 140). A further, but relatively much smaller increase in T.P.V. associated with a large increase in 'chlorophyll a' was recorded during the late summer of 1967 and was due to a growth of Tribonema spp. see page 138.

For the period from January until May 1966, the T.P.V. was not measured, but from phytoplankton counts for this period it was apparent that the standing crop was small. The vernal diatom bloom was not so obvious as that of either of the subsequent years, 1967 and 1968.



Although on the basis of Sverdrup's critical depth concept, it seems unlikely that production in the reservoir was ever completely limited by insufficient light and very turbulent conditions, it is very probable that the size and the rate of change in the standing crop were profoundly influenced by these factors. At times however, other factors including the rate of inflow and thus outflow; temperature, nutrients and biotic factors were equally if not more important. In the Spring of 1967 and 1968, the initial increase in the standing crop was associated with the increases in day length and the total recorded incident radiation when the light intensity was apparently approaching a saturation value (see page 51) at least in the upper 1-3 metres of water. In both years there was a gradual increase in the turbulence index value preceeding and during the initial stages of the spring 'growths', but in 1968, the maximum index value was recorded before the observed phytoplankton maximum and not, as in 1967, coincident with this peak.

Thus it would seem that the conditions in Sverdrup's concept for the initiation of a bloom after stabilization of the water column was not applicable at these times. Instead it is apparent that the beneficial influence of the imposed turbulence on production was due to its effect in maintaining a rate of circulation which transported the phytoplankton crop into and out of the high light zone in such a manner that the crop photosynthesis was more

efficient than it would have been under natural turbulent conditions.

The continued increase in the standing crops for both years was probably due to different factors. In 1968, a reduction in light penetration (see changes in water transparency in figure 6 ) occurred as the crop increased so that, even though the incident radiation was still increasing, it was very possible that the depth of the euphotic zone remained static or perhaps even decreased. Under such conditions, a further positive increase in the observed crop could only have occurred if there was an introduction of 'new' cells from an external source i.e. through the river inflow, or if the depth of mixing and thus also the turbulence were reduced.<sup>4</sup>

These conditions were apparently met, since a large inoculum of cells was introduced in the inflow, before the rate of inflow was reduced. This subsequent reduction in inflow, associated with a decrease in the imposed turbulence (as indicated by the decrease in the index value) probably accounted for the development of a thermal gradient. This would suggest that there was some stability in the water column and therefore some reduction in the depth of mixing so that maximum production and growth was probably restricted to the upper layers, while much of the heavy and larger cells and detritus sedimented out into the lower layers.



However, in 1967, conditions were completely different, since the water transparency was low throughout the previous winter period and thus any reduction in light penetration during the increase in the standing crop was masked. Therefore the depth of the euphotic zone was probably considerably less than in the corresponding period in 1968 and possibly remained fairly constant or even decreased throughout the phytoplankton increase. It seems very likely that the continued increase in the crop was the result of both the continual, beneficial effect of the imposed turbulence and the boost to the cell numbers by the continual introduction of fresh inoculum from the river inflow. A marked decrease in the standing crop was associated closely with the reduction in the turbulence index and the onset of water stabilisation (indicated by the development of a thermal gradient) and is considered to be further evidence that the crop maximum was not due to growth of the organisms. In 1968 however, the phytoplankton crop did not decrease immediately after the reduction in the index and thus imposed turbulence. Therefore it seems likely the observed increase in the crop was due mainly to growth and not entirely to the accumulation of numbers by continual resuspension.

While turbulence was considered to be an important factor, the decrease in the standing crops in both 1967 and 1968, was probably due to the interaction of several factors including nutrient

limitation and biotic factors, (~~see page~~). The absence of a large standing crop of spring diatoms in 1966 may also have been partly due to these physical factors of inflow, turbulence and water stability.

Throughout 1966, the rate of inflow was maintained at 40 millions of gallons/day or less which was considerably lower than in either of the following two years. As a result of this low flow there would be an expected decrease in the size of inoculum introduced into the reservoir from the inflows. However, the maximum crop of phytoplankton in 1966 was not observed in the river until early June so that the spring crop of diatoms was small compared with that in either 1967 or 1968. Thus comparatively few cells were introduced into the reservoir population from the inflows during the spring months of 1966. The low rate of flow and the inlet/inflow system in use at this time were responsible for a low imposed turbulence since the mean index value was 20 which gradually decreased from mid-April to 7 and 8 in June 1966. Thus during the early spring months when the incident radiation was insufficient and the turbidity too high to maintain a deep euphotic zone in the reservoir, the total turbulence (natural + imposed turbulence) was probably just sufficient to circulate the plankton at a rate, in and out of this zone, which would effectively impair the overall rate of production, and not improve it.

A reduction in the overall turbulence from mid-April and the development of thermal gradients although the overall temperature was low was associated with a slight increase in the standing crop,

but it was apparent that the small river inoculum was sedimented out on to the bottom of the reservoir without remaining in or even reaching the euphotic zone. Similarly several of the larger and heavier species of plankton diatoms e.g. Stephanodiscus astra probably dropped out of the zone through lack of turbulence. It seems possible that the lack of a large standing crop during this period was in part, due to the absence from the euphotic zone, of a sufficiently large initial inoculum of some species capable of exploiting the environment. However, in late June and early July, the stability of the water column, depth of the euphotic zone and the level of the incident radiation were such that the conditions for blooming formulated by Sverdrup (1953) were fulfilled and thus resulted in a large development of phytoplankton standing crop composed mainly of Tribonema spp. and Fragilaria <sup>on</sup> crotensis. The decrease in this crop occurred soon after a change had been made in the inlet system (see page 45) which was associated with an increase in the imposed turbulence (as indicated by an increase in the index value to 15). It seems very likely that most of the standing crop, especially the non-motile Fragilaria, was forced out of the euphotic zone by the induced circulation and sedimented onto the bottom of the reservoir. At the peak of the crop, the nutrient levels in the upper layers of water were considerably reduced so that it is probable that the plankton production was declining even before the enforced sedimentation. Thus the population, already moribund, could not

adapt to these conditions and quickly started to decay (see Ridley, Cooley and Steele, 1967).

The only large increase in standing crop to occur during the winter months, in the course of this study, was observed in October until December 1966, and it was due to the growth of Coscinodiscus rothii. Halldal (1953) reported that species of Coscinodiscus were the only centric diatoms to be regularly recorded in the winter plankton of the Norwegian Sea. It is also apparent from the work of Jenkins (1937) and that of Parsons (1965) that several species of this genus show low light adaption. Thus, although there is considerable variation between different species and even between different races of the same species, so that generalisations should not be made, it does seem possible that the reservoir species may well have been adapted to low light intensities. However, it seems very likely that the occurrence and persistence of this diatom was closely dependent on the conditions of turbulence and physical factors in the reservoir.

Coscinodiscus ref. rothii was not recorded in the river inflow before or during its growth in the reservoir. Instead it seems probable that an inoculum of viable cells was present in the sediment at the bottom of the reservoir. These were brought into the upper layers of water and an adequate light regime, through the resuspension of sediment by the change to horizontally placed jets in



September and October. The rate of circulation induced by the imposed turbulence was probably sufficient to prevent resédimentation of the cells out of the euphotic zone for long periods so that there was overall net positive production. The size and persistence of the crop was the result of both cell growth and cell accumulation and the gradual decline in the crop to the cessation of further growth and slow loss to the bottom and outflow.

From the preceding account it seems very probable that turbulence can be an influential factor in the development, persistence and decline of large phytoplankton increases. Its effect may be beneficial or detrimental and could at times, be the deciding factor in the situation for dominance of one species over another. Although there is still much research required on the interaction of phytoplankton between themselves and their environment the Q.E.II reservoir and other similar reservoirs, in which the inflow and imposed turbulence can be controlled, offers an ideal environment for this type of research. It is also of great use since, although the calcareous and alkaline waters are extremely eutrophic, nutrient limitation need rarely be considered as an important factor in the reservoir, and thus complicate and modify the environment. Thus the environment of the Q.E.II reservoir can be considered as similar to any lacustrine situation, but slightly more controlled.

Chemical Results and Discussion

The Thames and its tributaries form a calcareous river system which probably has the most eutrophic and perhaps the most polluted waters in the British Isles. Routine chemical analyses for some of the major ions in the Thames, by the Metropolitan Water Board (see Taylor 1965-1966) have shown a marked and continual increase in pollution since the beginning of the century. The river-filled storage reservoirs in the Thames Valley, are therefore, highly eutrophic although the chemical environment in each basin will be more or less influenced by the river conditions depending on whether it is a standing reserve or supply reservoir.

The seasonal variation in three dissolved inorganic nutrients - phosphorus, nitrogen and silicon - was investigated to determine the effect of a continual supply of river water on both the chemical and biological environment of the Q.E.II Reservoir. Concentrations of each nutrient have been reported in milligrammes/cubic metre, or as milligramme/litre.

Phosphate - phosphorus

The concentration of the dissolved phosphate-phosphorus in both the River Thames at the Walton intake and in the Q.E.II Reservoir was determined at regular intervals - weekly during 1966 and then fortnightly during 1967 and 1968 - for the period March 1966 until May 1968. A comparison of the seasonal variation in the concentration of this nutrient in the inflow and the mean



concentration for the reservoir (i.e. the mean concentration from the seven depth samples) is given in figure 7 <sup>following p. 99.</sup> During the investigation, the maximum concentration observed in the river was 2.01 mg/l (2010 mg/m<sup>3</sup>) on 19th July, 1966 and the minimum of 0.46 mg/l (460 mg/m<sup>3</sup>) on 30th March, 1966. However in both 1966 and 1967, the mean level of phosphate-phosphorus was greater in the last six months of the year than in the first six, although the yearly mean concentration in 1967 was 1.21 mg/l (1210 mg/m<sup>3</sup>) as compared with 1.308 mg/l (1308 mg/m<sup>3</sup>) in 1966. It is possible that this was due, at least in part, to total flow of water in the river, since there was apparently an inverse correlation between the concentration of this chemical and flow rate in the river (indicated by discharge of water over Teddington Weir, see page 35). A similar explanation probably accounted for the mean concentration in the river during January - May 1967 (1350 mg/m<sup>3</sup>) being higher than in the corresponding period in 1967 (1006 mg/m<sup>3</sup>) and in March to May 1966 (0.998 mg/l). Swale (1964) also reported an inverse correlation between phosphorus and flow rate in the River Lee, but Hrbáček et al (1966) and Smith (1959) as reported in Hrbáček (1966) found ~~that the~~ total phosphorus to be positively correlated with flow. This apparent contradiction may be partly resolved, however, by considering ~~that~~ the source,

form and level of phosphorus. In this investigation only the dissolved inorganic fraction of phosphorus was determined, whereas in both Hrbacek and Smith the total (inorganic and organic soluble fractions as well as the sestonic fraction) phosphorus was measured. It is generally agreed that the inorganic soluble fraction may represent only a small but variable portion of the total (see Hutchinson, 1957 and also Rigler, 1964) and therefore it might be, that if determined for in the River Thames a positive correlation would be found between the total phosphorus (P) and flow rate. The mean concentration of the dissolved inorganic fraction in the River Thames was found to be at least one and usually two orders of magnitude higher than concentration of the total phosphorus in either the River Vltava (Hrbacek) or the brook sampled by Smith. Neel (1951, reported by Hrbacek 1966) concluded that the rain had a flushing effect on the soil of the drainage area but it is probable that concentration of phosphorus in the rain could also have an additive effect (see Bellinger, 1968). Thus in such rivers as the Vltava and also other bodies of water of low phosphorus content, the high flows from rain and run-off would only serve to increase the content whereas in waters of high phosphorus content the reverse effect of dilution is more probable. Much of the phosphorus in the River Thames is probably derived from urban effluents (see note on Water pollution Min. of Tech. 1968,

42nd Report of the Metropolitan Water Board 1965-66) whereas this is less true of the River Vltava and unlikely for the brook described by Smith. Thus in the Thames during the summer months a reduction in flow, and therefore total volume of water would be expected to be related to an increase in the phosphorus content. A similar explanation may be applied to correlation reported by Swale for the River Lee (1964).

The seasonal variation in dissolved phosphate-phosphorus in the River Thames was not very marked when compared with the variations described in water bodies of low content e.g. some of the lakes in the Lake District (Heron 1961), but there was a distinct increase in concentration during the summer months of both 1966 and 1967. A similar summer increase was reported by Blum (see Blum 1956) in some American rivers. Although in the Thames this was probably due to the effluents and the reduction of flow as suggested above, a general increase in biological activity during the spring and summer may well have been in part, responsible. Distinct decreases in phosphate concentration were often associated with large increases in the phytoplankton standing crop e.g. at the end of August 1966 a decrease of  $580 \text{ mg/m}^3$  was associated with a large crop of Stephanodiscus astrea, similarly in late August and early September 1967, there was a decrease in phosphate associated with crops of small centric diatoms as well

as Stephanodiscus astraea, (~~see page~~)

The minimum observed concentrations of phosphorus were recorded during the winter periods when the flow rate was high and thus an association between concentration and standing crop, especially spring diatom crops in 1967 and 1968 which were usually larger than the summer crop, was not ~~obvious~~ obvious. During the period March 1966 until mid August 1967, observations were made on the concentration of phosphorus in the outflow from the reservoir. The mean concentration in the outflow was 1.15 mg/l compared with a mean of 1.055 mg/l in the reservoir and 1.04 mg/l in the river inflow. Apparently phosphorus was lost from and not retained in the reservoir which is contrary to the situation in the Slapy reservoir and other lakes and reservoirs reported in Hrbacek (1966). A possible explanation is that most of these lakes and reservoirs are considerably greater in volume and have much longer renewal times (i.e. time required by the inflow to completely refill the basin or exchange the existing water) than the Q.E.II reservoir so that phosphorus may be lost to sediments. The increase in phosphorus in the outflow might be partly due to biochemical or possibly purely chemical degradation and transformation of other forms of phosphorus. However, in the Q.E.II reservoir, the water can be drawn from several different depths at the outlet pier and also from

the outlets situated in the floor of the reservoir near to its centre and this could account for the differences, which did not generally exceed 10%, observed between the concentration in the outflow and the mean level in the reservoir.

Although there was not a distinct seasonal variation in the mean concentration in the reservoir, the average of the means for March to May 1966 ( $980 \text{ mg/m}^3$ ) and January to May 1967 ( $1040 \text{ mg/m}^3$ ) were slightly lower than the averages for June to December for both years and also for the corresponding period in 1968 ( $1250 \text{ mg/m}^3$ ). It is probable that both the rate of inflow into the reservoir and the mean concentration in the inflowing water were partly responsible for this effect. However it seems likely that there is not a serious depletion of oxygen at the mud-water interface until mid-summer, if at all, in the reservoir (see page<sup>97</sup>) and thus it is probable that much of the 'bound' phosphorus could be lost from the water to the mud and not released until late in the year. Similarly in 1966 when the imposed turbulence was thought to be low, much of the inflowing water might well have been retained in the lower strata of reservoir water and thus the phosphorus effectively 'locked up'. Such a situation would account for the observed average level of phosphorus being lower in March-May 1966 than in January-May 1967 although the levels in the inflowing water were respectively  $1.006 \text{ mg/l}$  and  $0.98 \text{ mg/l}$  for the same



period of time. Except for the period late June to mid-July 1966, the phosphate-phosphorus was apparently evenly distributed throughout the depths, and the differences in the observed concentrations in the surface and bottom samples did not exceed 20% and were usually much less, although sometimes but not always the higher concentrations were observed in the surface samples. A combination of imposed turbulence and biological activity were probably responsible for these differences, but continual replenishment and water exchange as a result of the inflow/outflow system, made the assessment of these factors difficult.



The range of phosphorus ( $\text{PO}_4\text{-P}$ ) concentration, recorded in the reservoir each year during the period of this investigation is shown in Table 3. The overall range of 80-1860  $\text{mg/m}^3$  for this period, is considerably greater - often one or two orders of magnitude - than that reported in many lakes and reservoirs (see Table 3). However, the range of concentration of phosphorus in waters polluted by urban and agricultural effluents is expected to be much higher than in uncontaminated waters (see Hutchinson, 1957). Thus, increased pollution in particular the introduction of synthetic detergents, (see Min. of Tech. Note 1968), has made comparisons between data collected before 1950 and after, increasingly misleading.

It seems very unlikely that the concentration in the reservoir would ever reach a limiting value although it is possible that during July 1966 in the upper layers of water it may have been approaching this value. During this period a marked phosphorus gradient developed through the depths associated with a thermal stratification and a large increase in the standing crop of phytoplankton (mainly Fragilaria crotonensis, colonial motile volvocales and some Tribonema sp. see page 133). As a result of the thermal gradient, replenishment from the lower water strata and inflowing river water was probably small so that the observed decrease in inorganic phosphate from 1.003  $\text{mg/l}$  to between 0.08 and 0.32  $\text{mg/l}$  in the upper 3 meters of water was probably a reflection of a real uptake through biological

# PO<sub>4</sub>-P in the Q.E.II Reservoir

TABLE 3A

YEAR	MAX. CONC.	DEPTH	DATE	MIN. CONC.	DEPTH	DATE
1966	1860 mg/m <sup>3</sup>	Surface	27th April	80 mg/m <sup>3</sup>	Surface	6th July
1967	1660 mg/m <sup>3</sup>	16.7 metres	9th August	500 mg/m <sup>3</sup>	13 metres	5th April
1968	1490 mg/m <sup>3</sup>	5 to 13 metres	25th May	1040 mg/m <sup>3</sup>	5 metres	6th March

TABLE 3B

## Range of phosphorus concentrations in diverse waters

LAKE/RESERVOIR	RANGE IN CONCENTRATION	REFERENCE
Q.E.II reservoir	80-1860 mg/m <sup>3</sup> (PO <sub>4</sub> -P)	Hrbacek 1966
Slapy reservoir	25-87 mg/m <sup>3</sup> (Total P)	Heron 1961
L. Windermere	0.1-3.7 mg/m <sup>3</sup> (PO <sub>4</sub> -P)	Ohle 1934
Baltic Lakes	5-600 mg/m <sup>3</sup> (PO <sub>4</sub> -P)	Rodhe 1950
Uppland Lakes	25-51 mg/m <sup>3</sup> (Total P)	

activity.

This decrease of some 700  $\mu\text{g/litre}$  seems unlikely to have been due entirely to phytoplankton - even 'luxury' consumption - since this would mean that the average cell content was about  $30 \times 10^{-9} \mu\text{g PO}_4\text{-P}$ , approximately fourfold the content reported for Asterionella formosa (Mackereth, 1953). It seems more likely that it was the net result of algal consumption, bacterial uptake and perhaps transformation into other non-determined forms, and general losses to the lower strata of water. However, similar but smaller decreases in dissolved inorganic phosphate associated with large increases in spring diatom crops were reported by Gardiner (1941) in Barn Elms No. 8 reservoir. It is possible, therefore, that there are different physiological races of species, ~~whether~~ genetic or purely adaptive (see Droop 1968), existing in water bodies of different nutrient status (see also Hutchinson 1957).

Decreases in phosphate were not always associated with increases in standing crop; e.g. from mid-September to mid-October 1966, and sometimes the decrease preceded the increase in crop e.g. spring 1967 which is in agreement with observations of Heron (1961) on some of the lakes in the Lake District. During the Spring 1968, there was a large increase in the standing crop composed mainly of Asterionella formosa, Stephanodiscus astraea and small centric diatoms, but the phosphate concentration apparently increased steadily throughout the period January - May 1968. However an estimate of the dissolved inorganic phosphorus budget for this period

suggested that there was an uptake of phosphorus within the reservoir of approximately double the uptake reported by Gardiner for Barn Elms in the Spring of 1938 (Gardiner, 1941). ~~(see page 71)~~. Continual replenishment by inflowing waters and the turbulent conditions within the reservoir probably accounted for the apparent observed increase by 'masking' the real uptake and it is most likely that there were other occasions in the reservoir during this investigation when changes in the observed concentration were not reflections of the real variations due to biological activity. Similarly, these factors are partly responsible for the dependence of the mean reservoir concentration on that of the river inflow.

Nitrate-, Nitrite- and Ammoniacal-Nitrogen

The dissolved inorganic forms of nitrogen - nitrate-N., nitrite-N., and ammoniacal-N. were determined in both the reservoir and the inflowing river water throughout the period March 1966 until May 1968. During this investigation, the predominant form was nitrate-N. and it accounted for 90-95% of the inorganic nitrogen while ammoniacal-N. represented between 4-9%. Nitrite-N., although present in detectable quantities in all samples, accounted for less than 2% of the inorganic nitrogen. A similar percentage composition for the dissolved inorganic nitrogen (considered from a comparison of the approximate mean concentrations for 1966-1967) was apparent from the seasonal distribution in these forms of nitrogen in the River Saale reported by Braune and Uhlmann (1968), although the range of concentrations of these ions was higher in the River Saale than in the River Thames. Prochazkova (1966) in her work in the reservoir Slapy, considered the mean percentage composition to be 80% Nitrate-N., 15% ammoniacal-N., and 1% Nitrite-N. which again is quite close to that suggested for the Q.E.II reservoir, but the maximum concentration of nitrate-N. in the Slapy was considerably lower than that in the Q.E.II reservoir. The higher percentage of ammoniacal-N. in the Slapy might be a reflection of the greater volume and depth of the Slapy and perhaps increased bacterial activity, although marked thermal stratification and summer stagnation and deoxygenation apparently does not occur in the reservoir (see Hrbacek and Straskraba 1966).



The concentration of Nitrite-N. recorded in the River Thames at Walton during the period March 1966 until May 1968, ranged from 3-180 mg/m<sup>3</sup>, but the annual mean concentration in 1966 of 71.5 mg/m<sup>3</sup> was greater than that in 1967, 40 mg/m<sup>3</sup>. A comparison of the mean concentration for the period March to May 1966 with that for the period January to May in both 1967 and 1968, confirmed that during this investigation there was a gradual but significant decrease in Nitrite-N. in the river, although the reason was not apparent. The fluctuations in the observed concentration in the river did not show any marked seasonal dependency, but in 1966, the lowest levels were recorded during the early summer. In the River Saale, however. Braune and Uhlmann (1968) demonstrated a seasonal variation in nitrite-N. with summer maxima and winter minima which they considered to be related to temperature and ammonification. Although there was not an obvious correlation between nitrite-N. concentration and rate of flow in the River Thames, the highest concentrations were recorded when the flow rate was low. It seems likely that this effect was incidental to the influence of flow rate on biological activity as well as the seasonal dependence of flow.

A comparison of the fluctuations in Nitrite-N. concentration, for the period of this investigation, in the reservoir and the inflowing river water is given in figure 8. The mean concentration in the reservoir was usually higher than that in the inflow but in



1967 and 1968 there was a gradual decrease in the difference between the mean reservoir concentration and that in the river. Both this decrease and the overall reduction in nitrite-N. level in the reservoir from 1966 until May 1968 might well be attributed, at least partly, to the general decrease in concentration observed in the river water and the increase in both the quantity of water input and thus throughput during 1967 and 1968 as compared with that in 1966.

During this investigation, the observed range of nitrite-N. concentration in the reservoir was between  $6 \text{ mg/m}^3$  and  $305 \text{ mg/m}^3$  and these values were recorded at 3 metres depth on 8th March 1967 and at 5 metres depth on 28th September 1966 respectively. However the annual mean concentration in 1966 was  $127.5 \text{ mg/m}^3$  compared with  $75 \text{ mg/m}^3$  in 1967 and  $54.2 \text{ mg/m}^3$  for the period January to May 1968.

Fluctuations in nitrite-N concentration with depth were recorded occasionally, but these were of short duration and varied distribution e.g. a clinograde distribution in nitrite-N. was observed in late June until mid-July 1966 at the same time as a marked thermal stratification (see page 45) whereas on both the 17th and 24th August 1966, maximum concentrations occurred at the bottom of the reservoir suggesting an inverse clinograde distribution (see Hutchinson 1957). For most of the investigation the nitrite-N. was evenly distributed or showed a slight gradient with depth, in which the difference in levels did not exceed 20%. When such gradients were

observed, the maximum concentration was sometimes recorded near the surface and at other times near the bottom of the reservoir, but the reason was not apparent. The mean reservoir concentrations were similar in value to those recorded in the Chew Valley Lake (Hamerton, 1959) but considerably greater than the concentrations observed in many lakes (as reported in Hutchinson, 1957).

Although high levels of nitrite-N. are usually regarded as signs of sewage contamination, this reasoning cannot be entirely applied to the high reservoir levels since it is apparent that these occur after impoundment. Instead it seems more likely that nitrite-N. accumulates in the reservoir through some break in the nitrogen cycle either because the rate of production is greater than the rate of transformation or that some organisms in the link between production and transformation are missing. It is generally considered that nitrite-N. is a transitional form during either nitrification or nitrate-N. reduction (Hutchinson, 1957) and that it is produced quantitatively from either ammoniacal-N or nitrate-N. Domogalla, Fred and Peterson (1926) and then Domogalla and Fred (1926) demonstrated that both nitrification and nitrate-reduction took place in the surface waters of Lake Mendota and the Lakes in the Yahara Basin throughout the year but their rates varied with season. The rate of nitrification was greatest during the late spring and at a minimum during mid-winter and late summer; while nitrate reduction was maximal during the late summer and minimal in winter

and spring, although there was evidence of a secondary maximum at the time of the autumn overturn.

There was a marked variation in nitrite-N. concentration in the reservoir during 1966. High concentrations were observed during March to mid-May and then the levels decreased through the summer to reach their lowest in July and August. A marked increase in nitrite-N. was observed in mid-August and maximal concentration was recorded at the end of September, after which there was a sudden decrease to the minimal winter levels. A similar, but much less obvious variation was observed in 1967, but the high spring concentrations were not apparent during 1968. This 'seasonal' variation contrasts distinctly with that for Lake Mendota described by Domogalla, Juday and Peterson (1925) in which there was a winter maximum and late summer minimum, and also for that described by Einsele and Vetter (1938) in the Schleinsee.

A probable explanation for this contrast lies with the physical environment of the reservoir. Much of the variation of chemicals in the water may be attributed to the physical conditions (e.g. temperature, turbulence and light penetration which are, themselves, dependent on season) either directly or through their influence on biological activity. In the reservoir, however, turbulence can be imposed through the inlet system and the water throughput, so that effectively the 'season' can also be altered and thus the 'seasonal' variation in chemicals.

During the increase in nitrite-N. in August and September 1966, both the concentrations of nitrate-N. and ammoniacal-N. decreased. An inlet change from 2 x  $22\frac{1}{2}^0$  jets to 2 x horizontal jets was made on 1.9.66. and then a third horizontal inlet was opened on 15.9.66. and these probably caused resuspension of some of the bottom sediment and the destruction of the inverse clinograde distribution of nitrite which had developed in August (see page 75). During this period there was an overall oxygen deficit, although the increase in the relative oxygen deficit was positive, (see page 99). The evidence from these observations suggests that, although there may have been a slight increase in nitrite by turbulent redistribution of the accumulated nitrite at the bottom of the reservoir (presumably at the oxygenated nitrate-rich and deoxygenated ammonia-rich interface) most of the nitrite was formed in the freely circulating water. A budget of the inorganic nitrogen, estimated at this time, suggested that observed loss in ammoniacal-N. was insufficient to account for the total increase in nitrite, but the overall loss in nitrate-N was much greater (see page 81) and thus it seems likely that while some nitrification probably occurred, there was more denitrification which may have partly resulted in loss of gaseous nitrogen. Such a situation agrees closely with the rate of denitrification observed by Domogalla and his co-workers (1926), and the observations of Pennington (1930).



However, the increase in nitrite-N. observed during September 1967 might well have been due to the oxidation of ammonia and not nitrate-N. reduction (but see page 86). Hutchinson (1957) concluded that "nitrite formation in the hypolimnion depended not only on the chemical conditions but also on the existence of a rather specialized bacterial flora which may develop transitorily over a limited depth range". It does seem likely that such a conclusion would apply for all depths of the Q.E.II reservoir.

There was not a marked seasonal variation in the concentration of nitrate-N. in the River Thames although the levels were usually lower in the summer months; but in both 1966 and 1967, the yearly minimum was recorded in the late winter or early spring. It is thought that drainage from agricultural land contributes much of the nitrate in waters and that very little is derived from sewage effluents (see Min. Tech. Note 1968), but there was only slight indication of a correlation between flow rate and nitrate concentration in the river. This may have been due partly to differences in run-off along the river course which would not necessarily be reflected in the flow over Teddington Weir (see page 35).

A range in concentration of 1.8 mg/l ( $1800 \text{ mg/m}^3$ ) - observed on 16th March 1966, to 8.6 mg/l ( $8600 \text{ mg/m}^3$ ) on 23rd March 1967 was recorded in the river, but the annual mean concentrations were 5.35 mg/l ( $3530 \text{ mg/m}^3$ ) in 1966. 6.74 mg/l ( $6740 \text{ mg/m}^3$ ) in 1967 and 6.11 mg/l



(6110 mg/m<sup>3</sup>) during the period January to May 1968. It seems very unlikely that nitrogen could ever be considered to approach a concentration which would be so low as to limit phytoplankton growth in the Thames, although there is some evidence (see page 82) to suggest that nitrate-N. is not always assimilated preferentially even though in the Thames it was always in excess of the other inorganic forms of nitrogen during the period of this investigation. The minimum recorded concentrations were not associated with large growths of phytoplankton. Rice (1938) also found that the phytoplankton pulse in the Thames was synchronous with high levels of oxidized nitrogen, but Roy (1955) described an inverse relationship between rainfall, phytoplankton and nitrate-N in the River Hoogly. This apparent difference in results may be associated with differences in nitrate concentrations in the two rivers and perhaps also the availability of other easily-utilized forms of nitrogen. The mean concentration in nitrate-N. in the Q.E.II reservoir appeared to depend closely on that in the river, although the levels in the reservoir were usually slightly lower and this difference was particularly noticeable during 1967 (see figure 9). Marked variation in nitrate-N. with depth were not usually recorded, but on both 6th July 1966 and 14th September a somewhat negative heterograde distribution with minimal concentrations in at 1 to 5 meters depth were observed. Surface concentrations of nitrate were sometimes

higher than the mean reservoir concentration, but there was no suggestion of replenishment through surface nitrogen fixation during the presence of Cyanophyta in the reservoir. Reduction in the nitrate concentration was not always associated with large increases in phytoplankton and this agrees with the observations of Prochazkova (1965) on the nitrate-N. concentration in the Slapy reservoir.

During August and September 1966, there was an observed decrease of 1.33 mg/l in the reservoir (although the estimated decrease, after consideration of water movement through the reservoir, was 1.17 mg/l,  ) which was considered to be due to bacterial activity since the phytoplankton population was small during this period. However in September 1967, there was a large population of Tribonema (see page 138) which was apparently associated with an overall increase in nitrogen. Even when the observed increase in reservoir nitrate-N. was corrected for replenishment from river inflow, the increase was apparently 94 µg/l which was probably due to oxidation of ammonia. It would seem that the rate of uptake of nitrogen was slower than that of production, although it is not possible to determine from these results in which form the nitrogen was assimilated by the algae. Ammoniacal-N. may have been utilized directly.

The evidence for the preferential assimilation of a particular form of inorganic nitrogen is usually circumstantial. Chu (1942) using algal cultures in the laboratory concluded that several freshwater species of algae were able to utilize nitrate in a greater range of conditions and dilutions than ammoniacal-N. Other workers (see Syrett, 1962) using laboratory cultures of mainly small chlorophyceae e.g. Scenedesmus spp., Chlorella spp., and Chlamydomonas spp. have demonstrated that usually both forms can be used, but growth inhibition may occur if the ammonia concentrations are high. Shilo and Shilo (1955) and Blinks (1951) suggest that the inhibition is correlated with an internal pH increase through the penetration of undissociated  $\text{NH}_4\text{OH}$  into the cell. However it is generally agreed that there is less energy required to assimilate the ammonium ion than the nitrate anion and thus it is, theoretically, to be preferred. Strickland, Holm Hansen, Eppley and Linn (1969) found that several marine species of diatoms and dinoflagellates utilised ammonium in preference when it was supplied in competition with nitrate and they concluded that this may be general in marine phytoplankton. This agrees with work on some freshwater species (as reported in Syrett, 1962). In an experiment with axenic cultures of Tribonema ? laequare, I supplied equal quantities of nitrogen (1 mg N./l) as ammonium-N., nitrate-N. and ammonium nitrate to different cultures whilst maintaining all the other elements in the

same proportions in the medium, but the pH was not adjusted. Maximum growth, and the most rapid, occurred in the cultures supplied with ammonium nitrate. In another experiment with Asterionella formosa in unialgal but not axenic culture, it was apparent that ammonium-N. was preferred. (~~see page~~). Several experiments have been carried out on natural populations of phytoplankton enclosed in bottles (e.g. Prochazkova, 1965) and plastic containers (Anita et al, 1963) and have shown uptake of both ammoniacal-N. and nitrate-N. as a preference, but the experiments were carried out at different times in the year. Dugdale and Dugdale (1965) demonstrated the uptake of both ammoniacal-N. and nitrate-N. in samples of water taken from Sanctuary Lake and enclosed in bottles to which N. labelled  $(\text{NH}_4\text{SO}_4)_2$  and  $\text{KNO}_3$  were added. Ammoniacal-N. uptake was greatest during the spring period although there was a smaller maximum in the autumn whereas the nitrate uptake was smaller than that of ammonia and occurred in the spring and late summer. They suggested that nitrogen fixation could occur at the same time as ammoniacal-N. and nitrate-N. assimilation and in the presence of both these forms, and thus was perhaps more useful for implementing the nitrogen resources than being the sole source.

A comparison of the ratio of nitrate-N. to ammoniacal-N. in both the river Thames and the Q.E.II reservoir with the <sup>maximum</sup> standing



crop of phytoplankton is shown in figure 11. Marked increases in this ratio were usually coincident with or immediately preceded, large developments of phytoplankton, and especially diatoms. While this does not demonstrate preferential uptake of ammoniacal nitrogen conclusively, it does suggest that ammonia was being removed at a rate relatively faster than that for nitrate-N. It seems unlikely that the increases in the ratio were due to increased nitrate-N. production.

The changes in the reservoir ratio did not closely reflect the changes that occurred in the river ratio. Instead, the maximum variation between the two ratios was associated with marked differences in the size of their respective phytoplankton crop, and was apparently not correlated with any other factor. This is considered to be further evidence for the removal of ammoniacal-N. by the phytoplankton or, perhaps, by a specialised bacterial flora associated with it.

Of the three forms of inorganic nitrogen studied, ammoniacal-nitrogen appeared to be the most obviously dependent on biological activity. There was not a distinct seasonal variation in concentration in the river although the higher concentrations of ammoniacal-N. were often recorded in the winter period. Since 'ammonia' is considered to be a major end product of the bacterial decomposition of organic matter, it seemed likely that it would be correlated inversely with flow. Instead there was not an obvious correlation which suggests



that much of the ammoniacal-N. in the River Thames might well have been derived from drainage run-off or directly from the rain (see Hutchinson 1957). Menzel and Spaeth (1962) also considered rainfall to be an important source of ammonia in the upper layers of the Sargasso Sea.

The ammoniacal-N. concentration in the Thames at Walton ranged from 0.111 mg/l (111 mg/m<sup>3</sup>) to 1.088 mg/l (1088 mg/m<sup>3</sup>), but the annual mean concentration in 1966 was 0.402 mg/l and in 1967 0.385 mg/l while during January to May 1968 it was 0.488 mg/l. These are considerably higher than that measured in the River Bourne in 1947 (Whitehead 1947) and the River Chew in 1951-1952 (Hammerton 1959) but similar to the concentrations in the River Saale (Braune and Uhlmann 1968).

The annual mean concentration of ammoniacal-N. in the reservoir was always less than for the corresponding period in the river - 0.242 mg/l in 1966, 0.355 mg/l in 1967 and 0.387 mg/l in 1968 - but the range of concentrations in the reservoir was much wider. The range varied from 30 mg/m<sup>3</sup> in the upper layers of water on 22.6.66 to greater than 1500 mg/m<sup>3</sup> in the bottom water on 20.9.67. This very high value was probably due to the release of ammonia from the sedimented organic matter under anaerobic conditions. During this period there were large amounts of organic matter (approximately 5000 mg/m<sup>3</sup>, ~~see page~~ ) in the inflows which may have sedimented out quickly; and the reservoir as a whole was markedly subsaturated with oxygen (see page 98). An estimated

budget for the dissolved inorganic nitrogen at this time - mid-August to the end of September - suggested that the overall increase in ammoniacal-N. in the reservoir was greater than  $705 \text{ mg/m}^3$  and that smaller increases in nitrate-N. ( $94 \text{ mg/m}^3$ ) and nitrite-N. ( $25 \text{ mg/m}^3$ ) also occurred which were possibly due to the oxidation of some of this ammoniacal-N. (~~see page 87~~)

These high levels of ammoniacal-N. may well have proved toxic to the growth of Tribonema spp. which was recorded during early September. The average value of pH in the reservoir is approximately 8.0 (see Annual Report (42nd) M.W.B.), but this could have been increased by the activity of the phytoplankton so that much of the ammoniacal-N. might well have been present as the undissociated  $\text{NH}_4\text{OH}$ .

A similar distribution in ammoniacal-N. was recorded during June 1966 when a range in variation of concentration with depth, of 30 to  $255 \text{ mg/m}^3$  was observed. Although the levels were higher in the bottom waters than at the surface, the cause was more probably due to removal at the top than release from sediments. During this period there was a marked thermal gradient so that circulation was limited and replenishment from both the inflowing water and the bottom layers was also slow.

During most of the investigation, however, there were not marked variations in concentration with depth, although at times,

especially during the spring and the winter 1966-67, distinct decreases in ammoniacal-N. were observed throughout the reservoir. Surface concentrations were not usually higher than those at other depths (see Hutchinson's explanation of Karcher's data 1939) and neither were they markedly lower during the summer months (see Juday, Birge and Meloche 1938).

The variation of ammoniacal-N. with depth and time in the Q.E.II reservoir is given in figure 10A and the seasonal variation in the mean reservoir concentration and that in the river is given in figure 10B.

Although there is a considerable quantity of inorganic dissolved nitrogen, as  $\text{NO}_3\text{-N}$ ,  $\text{NO}_2\text{-N}$  and  $\text{NH}_4\text{-N}$ , the total nitrogen content of both the reservoir and river waters may well be substantially greater, and on the increase. Thus although it is not possible to determine the ratio of the total nitrogen to the total phosphorus, the ratio of the dissolved inorganic ions - the ratio of  $(\text{NO}_3\text{-N}) + (\text{NH}_4\text{-N}) + (\text{NO}_2\text{-N})$  to  $(\text{PO}_4\text{-P})$  - ranged between 2.2:1 and 5.15:1 in the Thames and between 2.7:1 and 12.6:1 in the reservoir. The values were highest in the early months of the year and lowest during the summer months in both waters. In both 1966 and 1967, there were also small increases in the ratio during the late autumn.

Pearsall (1923, 1930, 1932) in his theory of periodicity considered the ratio of  $\text{NO}_3\text{-N} : \text{PO}_4\text{-P}$  to be important, but Rodhe's experiment (1948) suggested that the ratio was incidental to the fall in nutrient  $\text{PO}_4\text{-P}$ . The ratio is therefore, more often used

to indicate which element is most likely to approach a limiting level. In an experiment with Asterionella formosa in unialgal but not axenic condition, I measured the amount of growth in response to varying concentrations of phosphate-phosphorus in different N. : P ratios. ~~(see page 87)~~ The results demonstrated that with lower concentrations of  $\text{PO}_4\text{-P}$ , growth depended on both the N/P ratio and the source of nitrogen whereas with an initial concentration of  $1000 \text{ mg/m}^3$  P. the ratio was not so important, although maximum growth apparently still occurred at a ratio of 10:1. This ratio is probably close to the ratio of these elements within the cells (see Strickland, 1960).

III.

2. Silicon dioxide (Silica)

Silicon dioxide (silica) was determined by a method based on that described by Dienert and Wandenbulche (1923). Although there is some doubt as to the exact nature of the silicon compound thus determined and also the form in which silicon occurs naturally, (see Hutchinson 1957), it has been assumed, for this investigation, that silicon dioxide (silica) represents the form most readily available to phytoplankton and in particular diatoms (see Lund 1965).

A range in silica concentration of 2.0 mg/l (2000  $\mu\text{g}/\text{m}^3$ ) to 17.0 mg/l (17000  $\text{mg}/\text{m}^3$ ) was observed in the River Thames at Walton during the period March 1966 until May 1968. The mean concentration during this period of 9.5 mg/l is slightly lower than that suggested for the 'average river water' by Livingstone (1963); but if the very low levels, correlated with large diatom increases are excluded, the mean concentration in the river would become closer to the world average of 13.1 mg/l. That the mean silica content of the Thames at Walton is greater than the content of other rivers e.g. River Bourne, mean 5.2 mg/l (Whitehead, 1947) and the River Itchen mean 4.0 mg/l (Butcher 1927) within the British Isles, may be attributed both to the alkaline nature of the water and the sedimentary bedrock of the drainage area (see Hutchinson 1957).



Although there was an apparent seasonal variation in silica content in the river with maximum concentrations recorded during the winter periods, the variation was closely associated with, and somewhat dependent upon, the seasonal changes in the diatom population. Marked decreases in silica concentration and the minimum levels recorded for the river were always closely correlated with large increases in diatoms, and especially the spring diatom crops. In the late spring 1966, a minimum of 2.5 mg/l ( $2500 \text{ mg/m}^3$ ) was recorded, in 1968 this was 2.0 mg/l ( $2000 \text{ mg/m}^3$ ) but in 1967 the spring minimum level was only 4.4 mg/l ( $4400 \text{ mg/m}^3$ ). A comparison of the silica content of the water and the total number of small centric diatoms present, given in fig 13, suggests that these low concentrations of silica are approaching a limiting value. Swale (1963) calculated that the silica requirement of  $10^6$  cells of Stephanodiscus hantzschii was 38.4  $\mu\text{g}$ . Since many of the small centrics in the river were probably this species, and the material used by Swale in her experiments was taken from the River Lee, a tributary of the Thames, it has been assumed that the small centrics in the River Thames would have a similar silica requirement. On this assumption it is unlikely that the population in spring 1966 would have increased more than fourfold, and in 1968, that the spring population could have more than doubled. Also it seems probable that the maximum

population, during these periods would not exceed  $10^8$  cells/l.

A similar situation of apparent silica limitation has recently been reported by Swale (1969) in the River Severn.

The point indicated by a small arrow in figure 13 represents concentration of silica associated with a relatively small population of small centrics (compared with the spring crops, see page 102) which was sub-dominant to a crop of Stephanodiscus astraea. Even when small centric diatoms dominated the river phytoplankton, there were other diatom species present e.g. Melosira varians, Diatoma vulgare, Nitzschia sigmaidea, which were small in number but considerably larger in volume than the small centrics and it was possible that increases in the centric diatom populations were curtailed by competition for the available silica with these larger species.

Although Jorgensen (1957) suggested that the limiting concentration of silica is between 0.03 and 0.04 mg/l and this was confirmed by Lund (1965), some 50 times lower than the minimum concentration observed in the river, <sup>a</sup> bioassay of river water during the spring 1969, supported the hypothesis that silica limitation does occur in the Thames (see page 115). Recovery from silica depletion in the river was often very rapid and usually within one or two weeks. At the present time, there is insufficient information to decide the real cause but there seems to be, however, several possible explanations. Firstly it is possible that there

is no growth within the main river course and that a flush of phytoplankton-rich, silica-depleted water enters the river from some backwater or lake and is carried downstream as a complete entity with little or no mixing with the river water. Secondly it could be that growth of phytoplankton does occur within the river and that a combination of factors, including redissolution of silica from dead and dying populations and the introduction of 'new' silica from drainage run-off, are responsible for silica renewal. However it seems most likely that both situations occur together although one or the other may dominate.

A single series of samples taken at different stations along the River Thames between Oxford and Egham (Surrey) on 19th April 1968 (just after the maximum spring diatom crop had been recorded at the river inlet at Walton) indicated that there was a large increase in diatom standing crop between Abingdon and Pangbourne and that between this latter station and Egham the crop density remained fairly constant. Although no definite conclusions can be drawn from these observations it seems that if there was a phytoplankton flush, it was introduced below Oxford. However it is also possible that the nutrient status of the water, enriched from urban effluents from Oxford, was at its maximum for diatom growth between Abingdon and Pangbourne and this, coupled with slow water movement (since the river meanders considerably in this area), resulted in an 'ideal' situation for phytoplankton growth and therefore population increase. This aspect is more fully discussed

in Chapter IV (see page 100). The silica content of the water samples was not determined so that the precise area of minimum silica concentration, and thus perhaps maximum silica utilization, remains unknown.

The variation in silica concentration in the reservoir, although considerably influenced by the content of the inflowing river water was also very dependent on the fluctuations in the diatom populations through their utilization. Although certain other phytoplankton algae are known to utilize silica e.g. Chrysophyta, they were present in such low numbers in the reservoir that it is unlikely that they had any marked effect on the silica concentration.

With the exception of late June and early July 1966, when a marked thermal and chemical stratification was observed in the reservoir, distinct concentration gradients with depth were not observed during the period of the investigation. In the June-July period a minimum concentration of 1.26 mg/l ( $1260 \text{ mg/m}^3$ ) was recorded at 1 metre below the surface on 6th July 1966, and the mean concentration in the upper three metres of water was 1.56 mg/l. During the rest of 1966, the mean silica content of the reservoir ranged between 6.6 mg and 12.2 mg/l ( $6600 - 12000 \text{ mg/m}^3$ ), and was considerably lower than the concentration observed in the inflowing water, apart from the period March to June, and then the last week in August. In the latter period this was due to a sudden decrease in the river concentration associated with a river diatom crop (see page 108) but it was of short duration. A combination of



silica utilization in the river, low flow rate of water into the reservoir and probably only slow exchange between inflow and existing reservoir water (since imposed turbulence was lowered during this period see page 45) may have accounted for the higher observed levels of silica in the reservoir during March-June 1966. At the same time there was probably very little utilization and uptake of silica in the reservoir water by diatoms since the recorded crop was small compared with the following years. However silica uptake during late October until mid-December 1966, by a population of Coscinodiscus rothii was probably, in part at least, responsible for the observed decrease in reservoir silica although the river content continued to be high. In addition to this, since the imposed turbulence was low throughout the winter 1966-67 after the change to Bellmouth inlets (see page 45) it is probable that there was only a slow rate of exchange between inflow and existing water in the reservoir, dependent on natural rates of overturn and turbulence, and thus the mean winter silica concentration continued to remain lower than that recorded in the inflow.

In the spring of 1967, the mean concentration in the reservoir dropped to a recorded minimum of 0.5 mg/l ( $500 \text{ mg/m}^3$ ) throughout the depths of 28th April, which was associated with a large diatom crop. Since this minimum was considerably lower than that recorded in the inflow, some uptake apparently by the diatoms



must have occurred. Although the concentration of silica in the reservoir then remained lower than that in the inflow during the rest of the year, except for occasional periods of sudden decreases of short duration in the river, the reservoir concentration gradually approached that in the river. It seems likely that this was due both to the rate of flow through the reservoir (the inflow being two to three times the quantity during 1966) and the lack of a large winter diatom crop. In 1968, the minimum mean silica concentration in the reservoir was 1.78 mg/l (1780 mg/m<sup>3</sup>) whereas that in the river was 2.0 mg/l which was recorded two weeks before the reservoir minimum. Since there was a large diatom crop in the reservoir, silica utilization was expected, but this was not immediately apparent from the observed decrease in silica which followed closely the decrease in the inflow silica. An estimated silica budget for the reservoir during 1968 (~~page~~) indicated that there should have been an overall loss of silica through the outflow of about 81600 kg - a decrease of 4.75 mg/litre in the reservoir. However, during this period the observed decrease was from 13.8 mg/l to 3.75 mg/l approximately 10.1 mg/litre and thus the uptake in the reservoir must have been about 5.3 mg/litre. Since the diatom crop was composed mainly of Asterionella formosa, Stephanodiscus astraea and small centric diatoms (see page 139) in concentrations of approximately 250, 500 and 4800 cells/ml respectively, it does not seem too

improbable that such an uptake was due entirely to these diatoms. It is also very likely that the standing crop was an underestimate of the total diatom population since many cells would have been lost to the outflow. ~~(see page 169)~~ On the basis of Jorgenson's work on silica limitation (Jorgenson 1957) it is unlikely that the silica concentration in the reservoir during the spring period reached a limiting level. However, there is some evidence from experiments carried out in both 1968 (on the potential growth rates of phytoplankton populations in the reservoir) and in 1969 on the bioassay of natural waters (see Chapter VI page 169) that the minimum silica concentration observed during these periods was approaching this value. For, although neither experiment can be used to indicate conclusively nutrient limitation, they both suggest that the factor limiting the crop production was chemical in nature.

Dissolved Oxygen in the Reservoir

The concentration of the dissolved oxygen in the samples collected at Tower A (see Fig.15) was determined as part of the routine sample analyses at the Metropolitan Water Board, throughout the period of this investigation. These results, converted into percentage saturation values, are given in the form of a depth/time diagram in figure 15 (preceding p. 124)

The observed saturation values ranged from a minimum of 60% recorded in several bottom samples (taken at a depth of 16.5 m) e.g. on 27th July 1966 and 24th August 1966, to over 300% in the surface and 1m samples collected on 6th July 1966. Although it was not apparent from these observations it is very probable that there were periods of marked oxygen depletion, near or at the mud-water interface during the course of this study and, particularly, in the summer months. Low oxygen concentrations (1 mg/litre) were reported in the outflow in mid-July 1966 (see Ridley, Cooley and Steel 1967), and at least one sample of mud collected during the summer of 1967 was anaerobic.

During the winter periods, when biological activity is at its lowest, the recorded saturation values were between 90% and 99% and on 17th January 1968, values of 100% were found at the surface and at 16m. These results were almost certainly due to the

circulation enhanced by the imposed turbulence of the jetting inlet system (see section III). Full saturation and supersaturated concentrations of oxygen were observed on several different occasions, but they were always associated with large standing crops of phytoplankton. In early November 1966, and both the springs of 1967 and 1968, supersaturation values were recorded throughout the depth of the reservoir whereas in the late spring and early summer of 1966, an oxygen gradient developed and supersaturation was restricted to the upper 11 metres of water. At the same time there was also a thermal and chemical stratification and these were almost certainly the result of a reduction in the imposed turbulence and the development of a large growth of phytoplankton in these upper layers (see figure 6).

However, during the early part of September 1967, the values of saturation did not exceed 86% even though a large increase in phytoplankton (Tribonema spp. see page 138) was recorded. It is possible that the population was not capable of a rate of photosynthesis comparable with that of the populations associated with supersaturation, but it seems more probable that the oxygen may have been used in biochemical oxidation; since saturations between 60% and 80% were recorded throughout the period of May until mid-October 1967. As the routine collection of samples was always carried out in the early morning (usually before

9.00 a.m.) it is also likely that the subsaturation was merely a reflection of the diurnal variation in oxygen.

Similar levels in saturation (between 60% and 80%) were recorded during July 1966, September to the end of October 1966, and at the end of May 1968. In July 1966, this was probably due to the biodegradation of the phytoplankton bloom (see page 134) and redistribution of the dissolved oxygen through the circulation imposed by the change in inlets, while during September - October the resuspension of organic detritus from the bottom of the reservoir and its eventual oxidation would account for the observed levels of oxygen. In May 1968, and also the period following the spring diatom increase in 1967, both the presence of large numbers of animals (Duncan, personal communication) and the dissipation of the phytoplankton bloom would reduce the oxygen content of the water.

If the oxygen values in the Q.E.II reservoir during 1966 and 1967 are interpreted in the way discussed by Hutchinson (1957) in relation to oxygen deficits (see table A , appendix 1 ) they suggest that the total oxygen consumption does not vary greatly through the summer and early autumn periods and that the observed variation in oxygen content of the water is mainly a result of the variation in biological productivity.



The seasonal variation in some of the major nutrients in the Queen Elizabeth II Reservoir (●—●) and the inflowing water from the River Thames at Walton (⊙-----⊙)

Fig. 7.           Variation in  $\text{PO}_4$  - P

Fig. 8.           "     in  $\text{NO}_2$  - N

Fig. 9.           "     in  $\text{NO}_3$  - N

Fig. 10.          "     in  $\text{NH}_4$  - N

Fig. 12.          "     in silica

FIG. 7

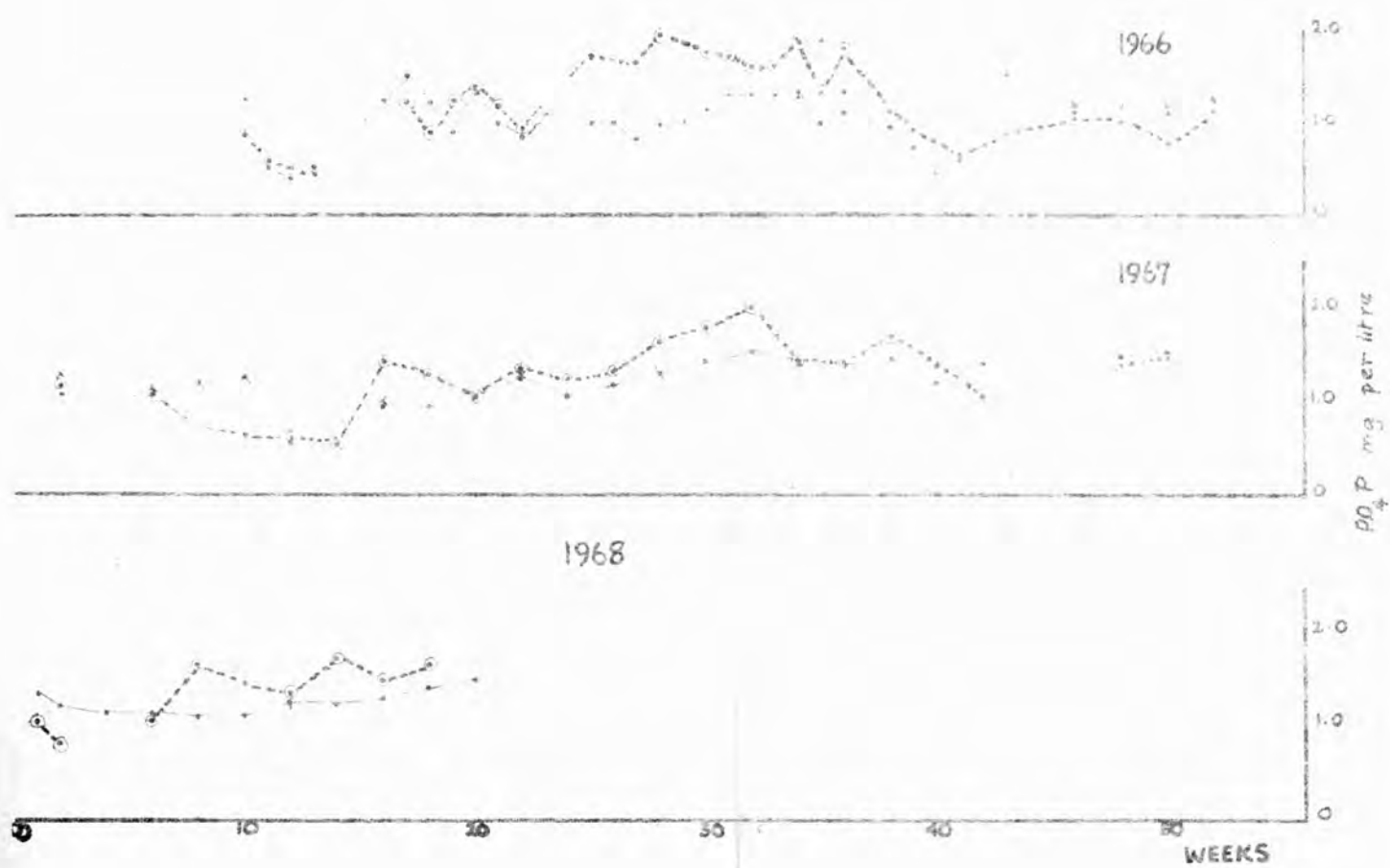


FIG. 8

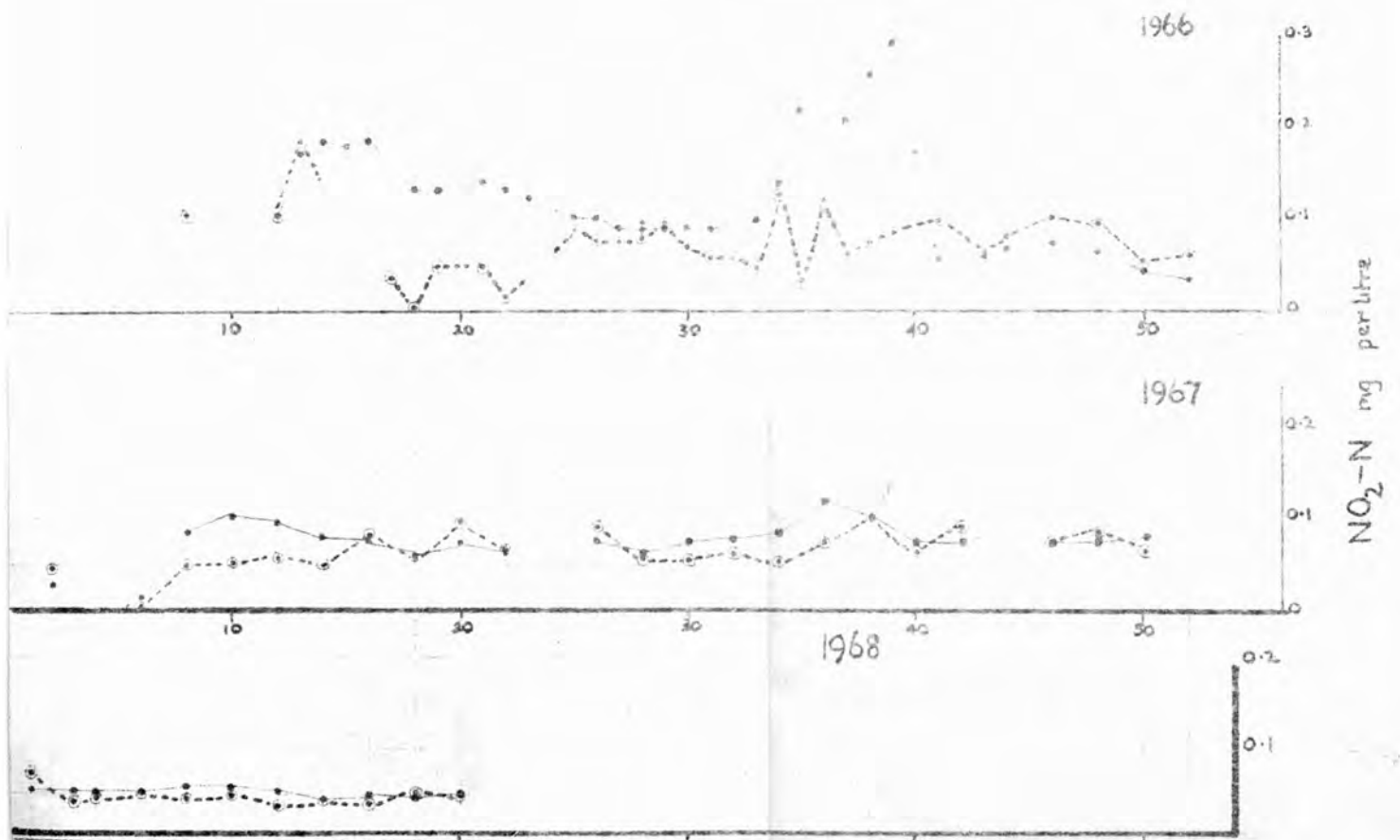


FIG. 9

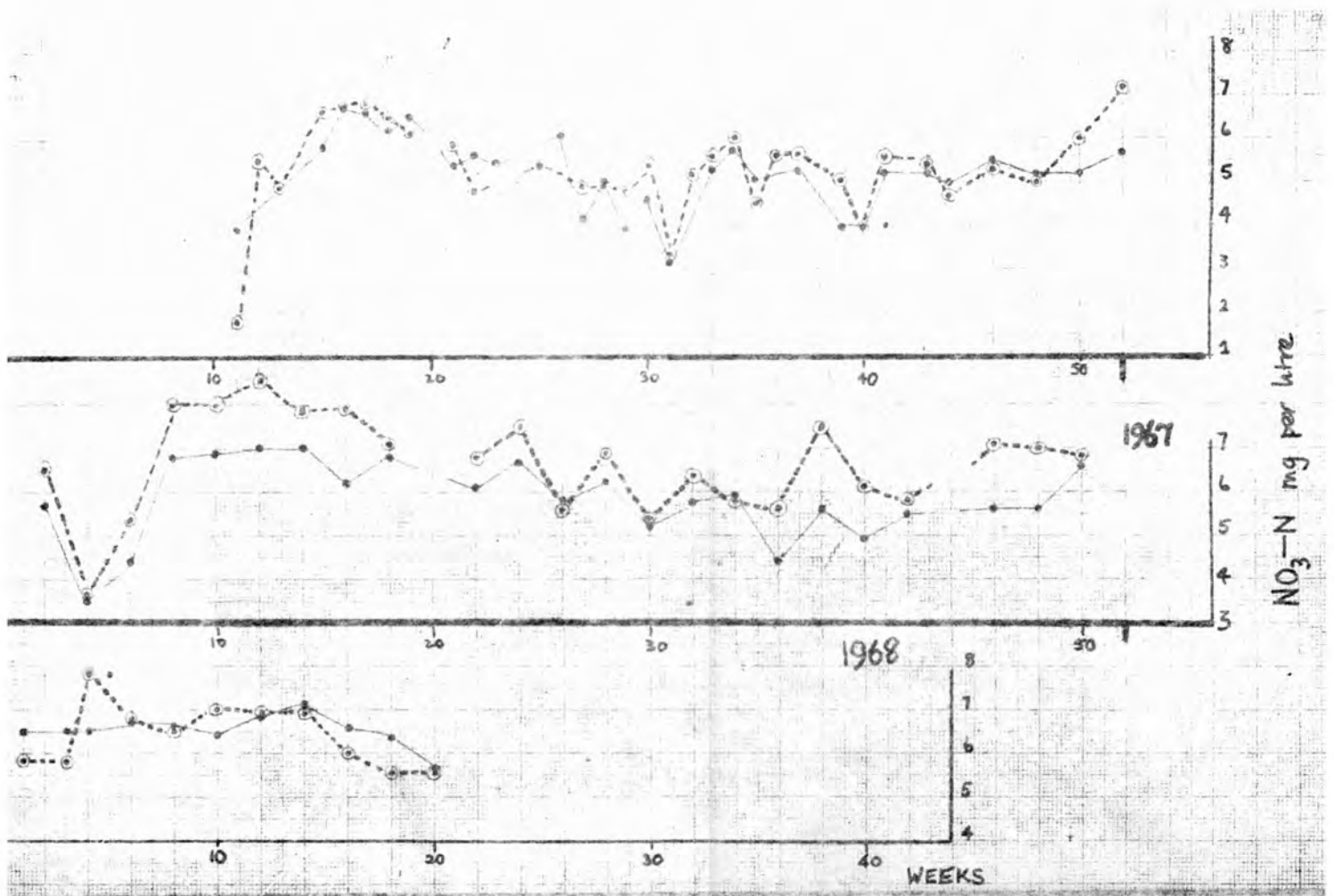


FIG. 10B

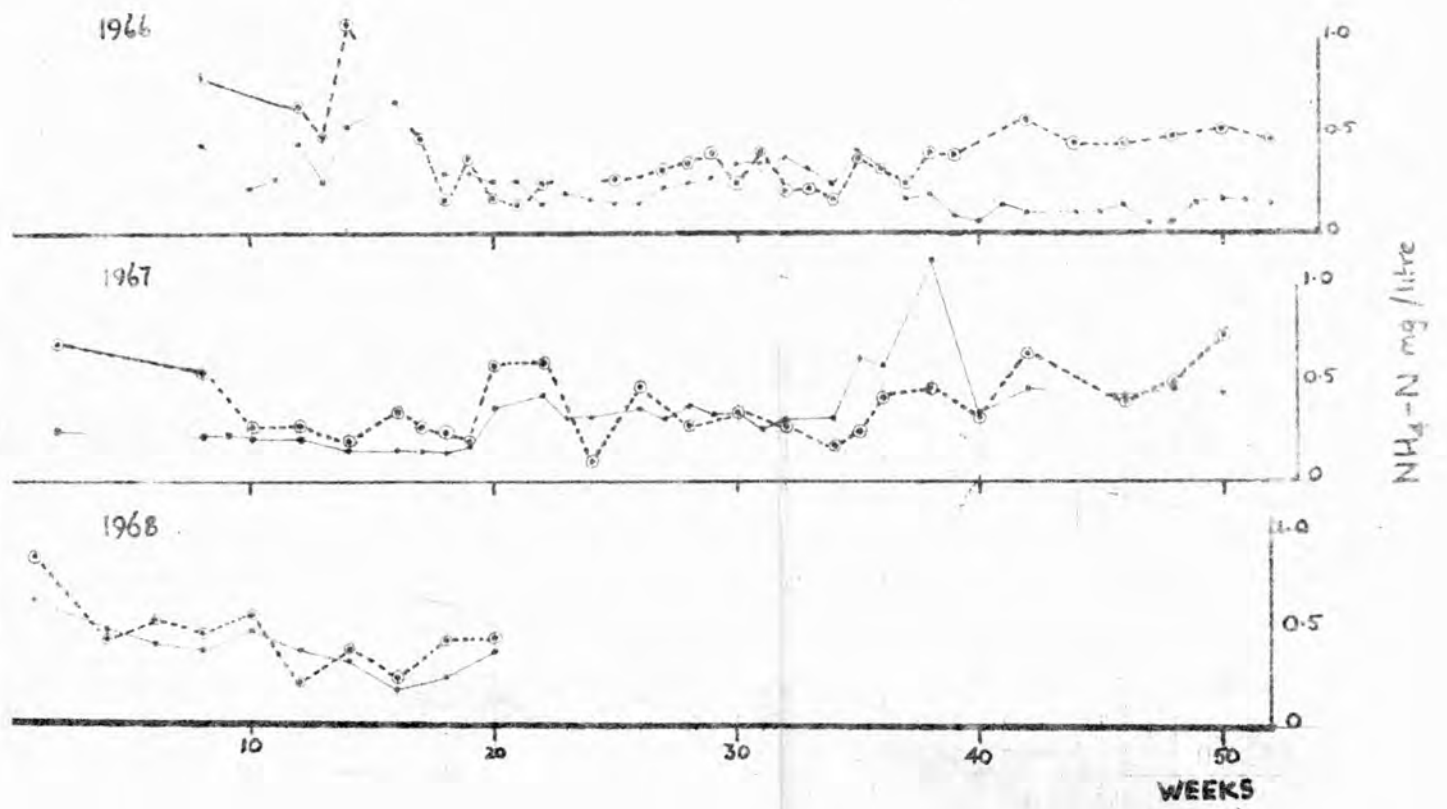




FIG. 12

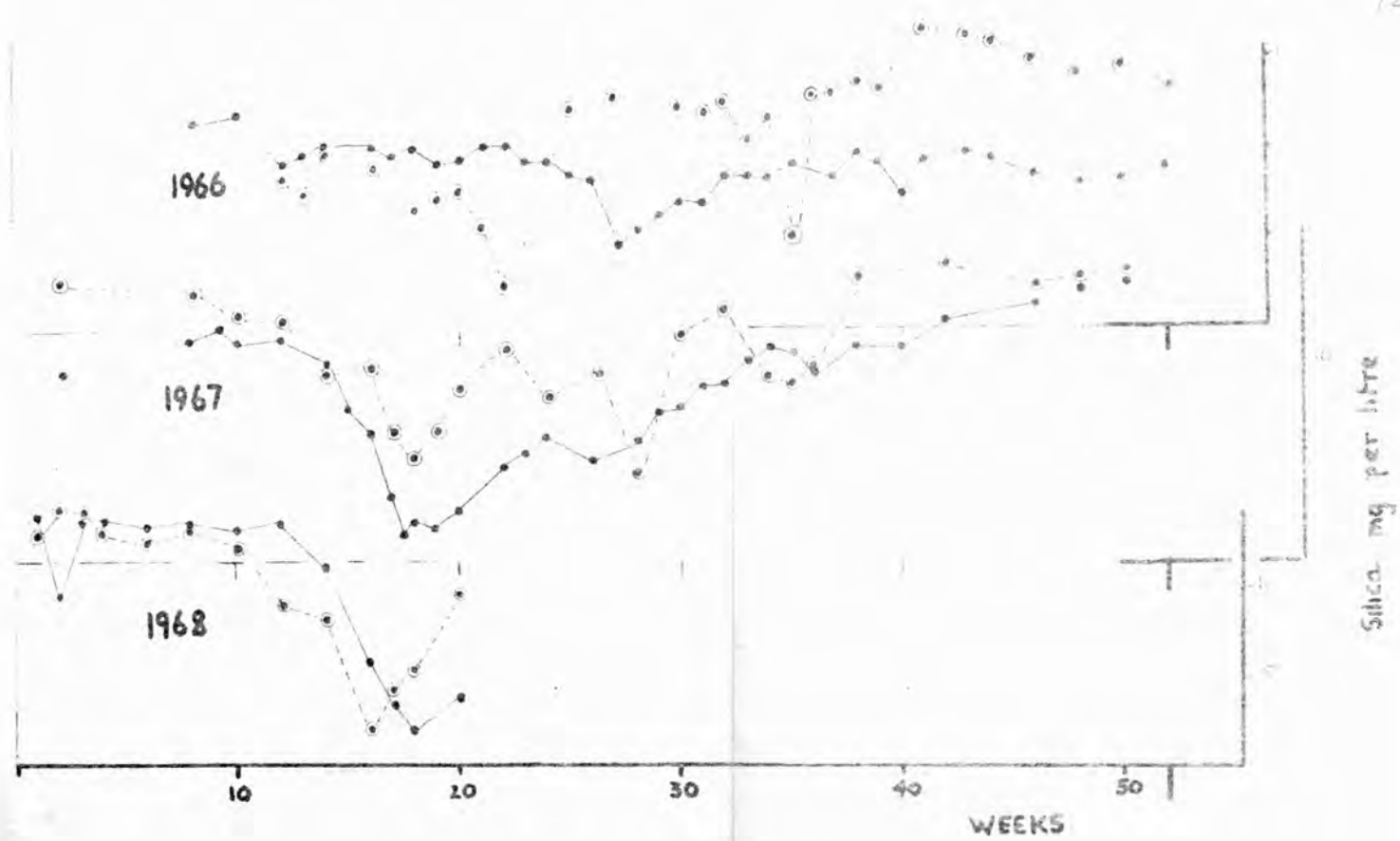
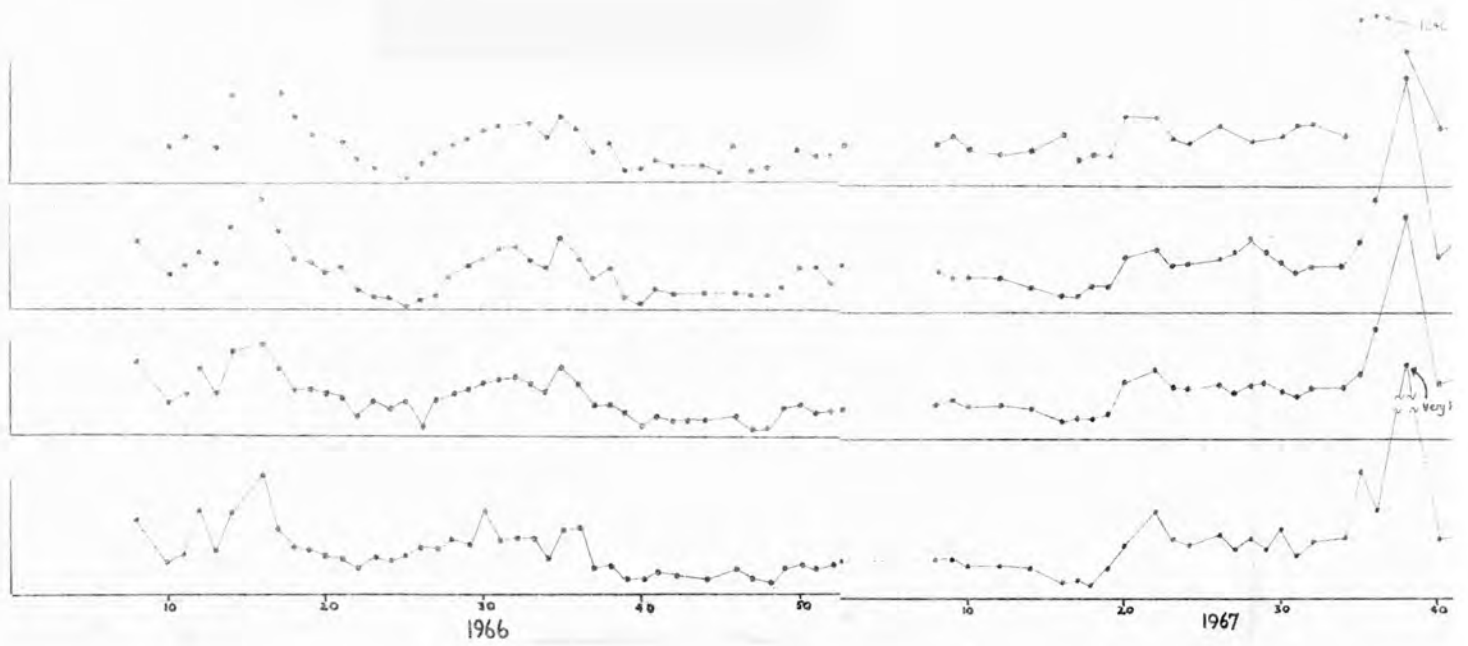
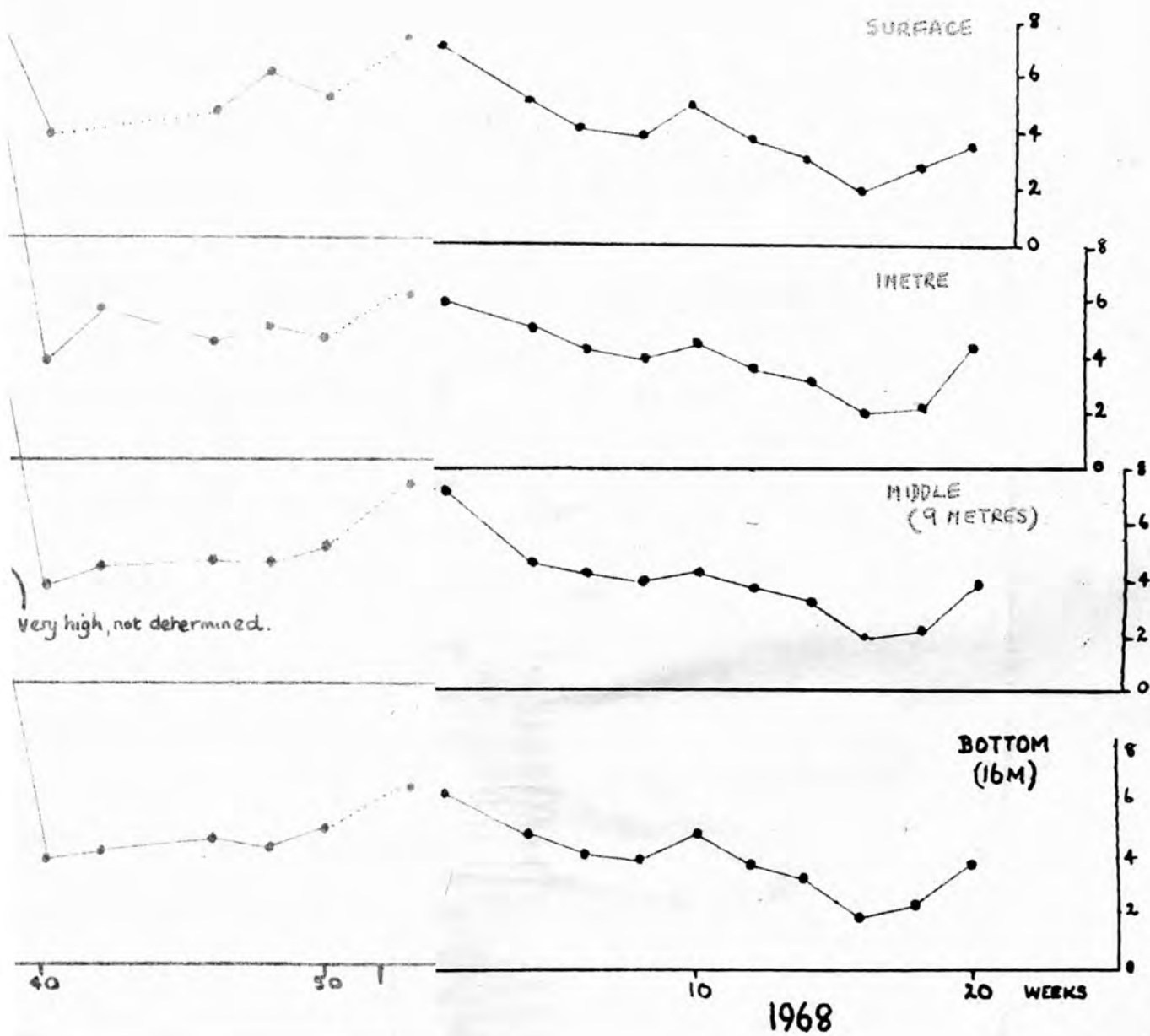


Fig. 10a Seasonal variation in the concentration of  
 $\text{NH}_4 - \text{N}$  at the surface, 1 metre, 9 metres and  
16 metres depth in the Queen Elizabeth II  
Reservoir.

88-100-101-102



1240  $\mu\text{g}$

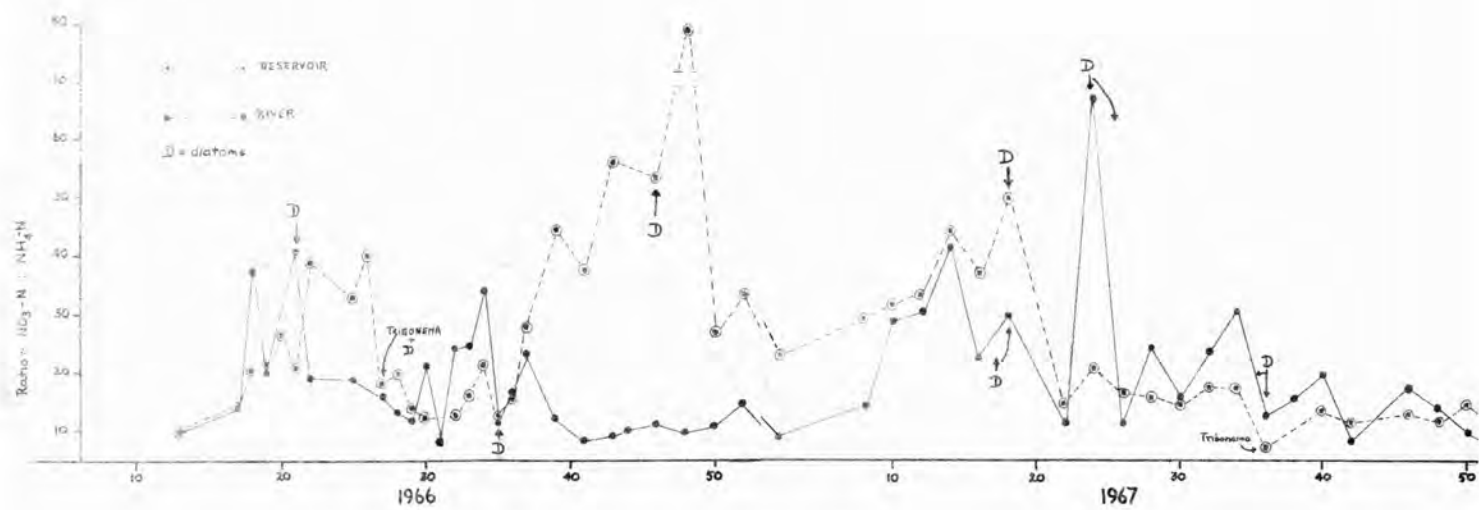


$\text{NH}_3 - \text{N} \quad 10^2 \mu\text{g per litre}$

Fig. 11. The variation in the ratio of  $\text{NO}_3 - \text{N}$  to  $\text{NH}_4 - \text{N}$  concentration in the Queen Elizabeth II reservoir ( $\odot - - - \odot$ ) and the River Thames inflow ( $\bullet \text{---} \bullet$ ). The periods of maximum standing crop are indicated by arrows. D indicates a standing crop dominated by diatoms.



FIG. 11



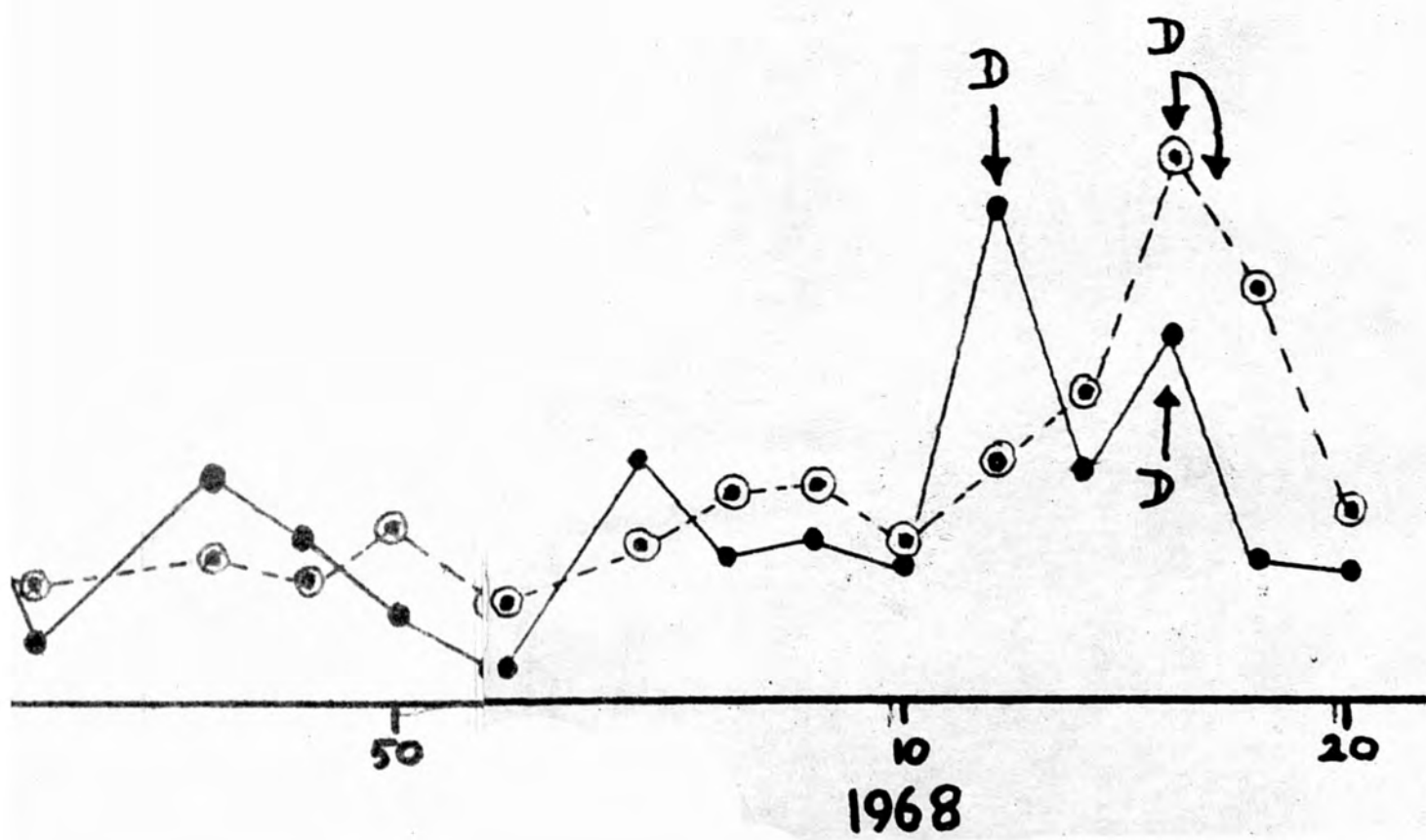
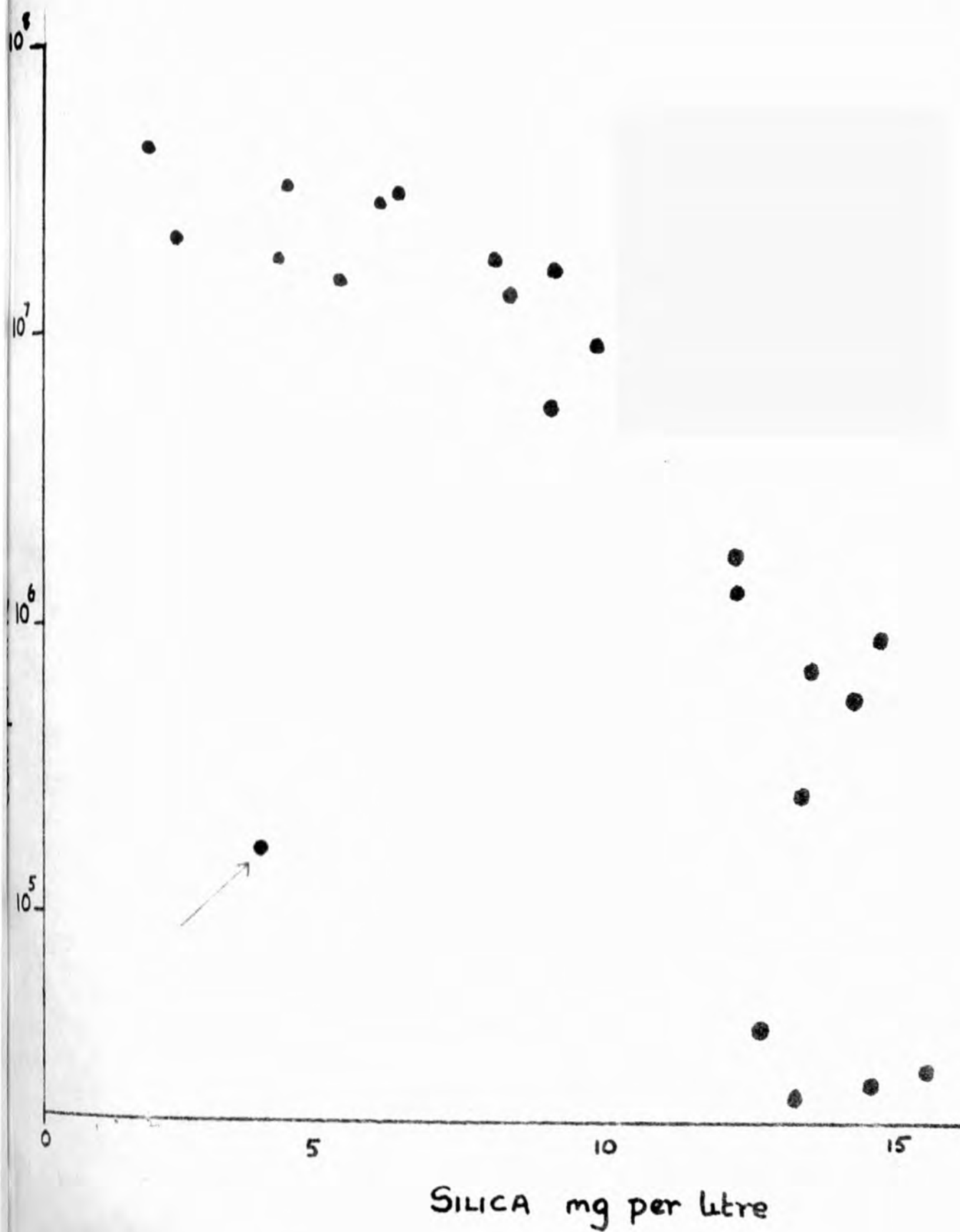


Fig. 13. The variation of silica concentration and numbers  
of small centric diatoms in the River Thames at  
Walton.

FIG. 13



Chapter IV

A. Phytoplankton in the inflow from the River Thames at Walton

Samples of river water were collected from the Walton Intake channel throughout the period January 1966 until May 1968. The presence of large amounts of detritus and silt in the river, especially in the winter and early spring months, made difficult the enumeration of phytoplankton by the Utermohl sedimentation technique in many of these samples. However, it is apparent from the several counts which were made during the winter periods and from other reports (see Annual Reports of the Metropolitan Water Board) that the standing crop of the phytoplankton in the winters was considerably smaller in both volume and species composition than either the late spring or summer crop.

During this investigation, more than 100 species of algae, representing eight classes, were identified and frequently recorded in the phytoplankton. However, less than 20 of these species - mainly Bacillariophyceae - occurred in large numbers and with the exception of samples in June 1966 and January 1968, the plankton flora was dominated by this class. In spite of this dominance, there was a distinct seasonal succession of species with the percentage of Chlorophyceae in the flora increasing during the summer months. Members of the Cryptophyceae were also common during the summer, but as a result of their persistence in the flora throughout the season, they accounted for a greater proportion of the standing crop in the

winter than in the summer. The Cyanophyceae were very poorly represented in the Thames flora and the other classes - Xanthophyceae, Chrysophyceae, Dinophyceae and Euglenophyceae - accounted for less than 1% of the phytoplankton crop although individual species in these classes occurred frequently in the samples. ~~The percentage composition of the Thames phytoplankton flora at Walton, during the period of this investigation is shown in figure 1 with the seasonal changes in the standing crop (expressed as the volume of the most abundant species) and the total particulate volume.~~

Small centric diatoms, including Stephanodiscus hantzschii, S. hantzschii var. pusillus, (which was particularly noticeable in river water cultures) S. astraea var. minutula and several Cyclotella spp., were the dominant organisms of the phytoplankton for most of each year. These small centric diatoms were found by microscope measurements to fall into three more or less distinct size populations, at about  $150 \mu\text{m}^3$ ;  $320 \mu\text{m}^3$  and  $600-720 \mu\text{m}^3$ . These populations together with Stephanodiscus astraea (cell volume range  $2000-4000 \mu\text{m}^3$ ) accounted for over 90% of the total diatom population, except during the winter months when it was probable that many of the diatoms in the samples were benthic forms forced into suspension by the very turbulent fast-flowing conditions in the river. <sup>Williams</sup> ~~Whithead~~ and Scott (1962) in their survey of the major water ways of the North American continent considered the genus Stephanodiscus to be of widespread occurrence and perhaps the dominant



or at least, most common genus in the phytoplankton. Similarly Stephanodiscus spp. and Cyclotella spp. apparently have a wide distribution in European rivers (see, for example, des Cilleuls, 1928-29; Lemmermann, 1907; Scholer, 1900 and Schroder, 1897); and in the relatively few published accounts of the phytoplankton in British rivers, other than the River Thames and its tributaries, these species (especially the smaller forms) appear to dominate or occur very frequently in the flora (see Swale, 1969, and probably the diatoms recorded in the River Chew by Hammerton, 1959).

Stephanodiscus hantzschii was recorded by Fritsch (1903) in his survey of the net phytoplankton in the Thames, and early Annual Reports of the Metropolitan Water Board (Harold, 1937; Mackenzii, 1938 and all subsequent reports) and Rice (1938) suggest that this species and the other small centric diatoms have been consistently present in the flora for at least 30 years and that they have been regarded as nuisance species for almost as long. Also Swale (1964) observed these species in the River Lee (a tributary of the Thames) and considered them to be the dominant organisms in the phytoplankton throughout the growing season.

It is clear that, from at least 1953 until 1966 (see Annual Reports for the Metropolitan Water Board, 1952-1966), the main increase in these small centric diatoms occurred between March and May each year, although they dominated the flora until late October or early November. During this investigation, the maximum numbers

of the small centric diatoms were recorded during April - May in 1967 and 1968 and later in May - June in 1966, when the concentration reached between 20,000 and 44,000 cells/ml., but they continued to be frequent and several smaller maxima (between 3,000 and 16,000 cells/ml.) were observed throughout the summer months until late October in both 1966 and 1967. In the winter periods these small centrals persisted in the flora but only in low concentrations.

There has been, however, little progress in determining the major factors controlling their growth or decline in this river, or even their distribution and geographical origin.

Swale (1963) showed that, under laboratory conditions S. hantzschii grew best in light of 5,000 lux (approximately  $3 \times 10^{-2}$  ly/min.) at 20°C. but was capable of good growth, after a lag period, even in light of 1,700 lux at 8°C. For this range of temperature - 8 to 20°C. - she suggested that the rate of growth for this species increased more or less regularly with increase in temperature.

Although laboratory results have limited application in the interpretation of field data, it seems more likely that the observed levels of incident radiation (from Kew Observatory see page 39) in both winter and summer would inhibit rather than limit growth of this species, and probably the other small centric diatoms, in the river. However, there can be little doubt that light after

penetration through the water is a major factor, in the seasonal variation of these diatoms (and other phytoplankton) in the river. There is some evidence - including the experiments on S. hantzschii by Swale; the suggestion by Rice (1938) that this species had a single summer maximum; and the changes in the small centric diatoms observed in the river during this study after the spring maxima - to suggest that S. hantzschii and the small centric diatoms have a similar growth potential to that demonstrated by Lund (1949) for Asterionella formosa. If this is so, questions arise as to the occurrence of the peak numbers of cells in the spring and early summer rather than later in the year and regarding the factor or factors determining the final concentration. It is possible, since it was not easy to identify the species during counts with the inverted microscope, that the observed fluctuations in the small centrics were due to different species or varieties on each occasion.. However, on several occasions when cleaned frustule preparations were made, S. hantzschii was apparently the dominant species, and only twice - once in mid-June 1967 and then in March, 1968, was the small centric population dominated by a very small (less than 5 $\mu$ m in diameter) centric diatom which could not be positively identified, but may have been possibly Cyclotella pseudostelligera (see the report by Bellinger, 1968).

It seems more probable that the answers to the questions depend on the interaction of several external environmental factors

and to a lesser extent on the inherent qualities of the population. A combination of factors including light availability, temperature, and high rates of flow and perhaps day length, prevent the initial increase in these diatoms until March each year. Since there was an inverse association, during this investigation, between increase in cell concentration and the rate of flow in the river, it is possible that this factor is of particular importance in determining both the time and the extent of the spring and subsequent increases. Flow rate will be effective in its influence on turbulence, turbidity and thus light penetration as well as circulating cells in suspension and perhaps by removal of most of the potential inoculum for new growths. Thus, it seems likely that the high rate of flow in the river during 13th to 20th April 1966 was responsible for the 'delayed' 'spring increase' until late May, by washing away most of the potential inoculum. Also the reduced rate of flow in spring 1968 compared with the previous years of 1966 and 1967 probably accounts for the larger maximum observed in this year and its occurrence at a slightly earlier date than 1967. Swale (1964 and 1969) has also considered that rate of flow in the rivers she has studied to be of great importance in influencing the phytoplankton population.

Lund (1965) suggests that reduced competition may favour the development of a particular alga at one time, even though suitable conditions for growth may occur at other times. Such a situation may well apply to the small centric diatoms in the spring

months and also account for the comparatively smaller maxima in the summer and autumn.

There was a marked and rapid decline in cell concentration after the spring growth in all three years, but only in 1967 did this coincide with an increase in the rate of flow. It is possible that in both 1966 and 1968, many of the cells sedimented onto the river bed as the rate of flow was reduced, although this reduction was not very marked. However, it does seem likely that the concentration of silica in the river during this period in 1966 and 1968 was approaching a limiting value and could have been partly responsible for the decline (see page 90). Although cells parasitised by chytrids were observed throughout the growing season, it is considered unlikely that either parasitism or heavy grazing can be regarded as major factors responsible for the decline.

In the present discussion it has been assumed that the observed increase was due to growth within the river basin, but there still remains the possibility that growth occurs elsewhere, for example in backwaters, and the observed fluctuations in cell numbers are due to discrete water masses moving downstream. In such a situation the observed decline merely indicates the boundary between two such water masses. Unfortunately there is no evidence for or against this hypothesis, although it does seem likely that there are definite 'zones' of plankton in the Thames. The survey along the Thames in 1968 (see page 123) does suggest this and Lack



(see report in Swale, 1969) considered that the dominant organism in the Thames plankton at Reading in 1967 was Stephanodiscus tenuis - a species which was virtually absent from the flora in the Thames at Walton. It seems very probably, in view of its heavily silicified frustules, that this species sediments out of the main water flow and on to the river bed somewhere between Reading and Walton and is therefore 'lost' from the plankton. This 'zonation' of phytoplankton and also the general movement of water downstream makes a real comparison of the phytoplankton changes from week to week difficult and perhaps even impossible. The clarification of the events leading to a phytoplankton pulse and then its decline in the river can only result from an extensive survey of the whole river system and the continual observation of a particular mass of water as it moves downstream. If the main growth and reproduction of the potamoplankton occurs within the backwaters or feeder lakes, ponds and reservoirs, the observed changes in the phytoplankton might well be expected to depend entirely on the physical river environment and biotic factors such as parasitism and grazing. However, if the potamoplankton is capable of reproduction as it moves downstream, a dynamic equilibrium with sedimentation losses compensated by cell division might well occur so that over long stretches of the river system there would be little or no apparent change in the cell concentration or composition.



Stephanodiscus astraea occurred most frequently in the late summer months in the Thames phytoplankton, although this species was present for most of the year except the winter period, and in 1968, it reached a concentration of about 250 cells/ml in the spring diatom crop. In both 1967 and 1966, the maxima were recorded at the end of August and the beginning of September when the cell concentrations reached 3,500 and 15,500 cells/ml respectively, and the flow rate in the river was near its lowest level for the year. In both years there was a marked decrease in silica concentration in the water, but in 1967 it was not possible to determine to what extent this decrease was due to the uptake by S. astraea and not by the small centric diatoms which dominated the flora. The decrease in silica in 1966 was about 7.0 mg/l, but if it is assumed that the frustule in S. astraea is approximately 10% of the total cell volume (in the river population about  $4,000 \mu\text{m}^3/\text{cell}$ ) (see page 143) this decrease is considerably lower than the calculated requirement by the population. Although this assumption may be completely incorrect, it is possible that either the population was developed upstream and kept within the phytoplankton by turbulence and that some silica replenishment has occurred as the water moved downstream to Walton or that, due to the reduced flow, much of the population was derived from the inoculum on the river bed in silica-rich water and is only in part dividing whilst in suspension.

It is particularly interesting to note that while S. astraea ref. "typica" (cell volume circa 13,000 - 16,000  $\mu\text{m}^3$ ) was recorded in the spring diatom crop in the reservoir in both 1967 and 1968, this "variety" was only very rarely observed in the Thames phytoplankton. The most probable explanation for this apparent absence is that in the spring light availability and the removal of potential inoculum prevent any obvious increase, while in the summer months the reduced rate of flow and thus turbulence is either insufficient to keep the inoculum in suspension or perhaps to remove the population from the river bed. There is, however, the possibility that mechanical damage to a cell of such volume prevents its survival and growth within the river basin, although no obvious signs of damage were observed. Stephanodiscus astraea var. minutula has been regarded as part of the 'small centric diatom' assemblage (see page 101) and therefore its occurrence has not been considered separately during the course of this investigation.

Species of Melosira were present in the Thames phytoplankton throughout the year, but showed specifically different periodicity. Melosira varians, the most common species, appeared to show both a spring and autumn maximum, while M. granulata and M. granulata var. angustissima were absent from the spring crop and occurred only in the late summer and early autumn. Rice (1938) reported a similar periodicity for both these species and suggested that there was a marked positive correlation between the occurrence of M. varians and

both the flood rainfall and the rate of flow in the Thames. It seems most likely that the spring increase was the result of the 'scouring' of cells from their substratum by the relatively high spring flow rate, whilst the autumn maximum was due, at least in part, to filaments moving into the plankton by flotation after intense photosynthetic activity. Such a movement was reported by Bellinger (1968) in the calm waters of filter beds and Kozhov (1955) in Lake Baikal. Intense production may well occur on the river bed (as well as on other substrata) under the reduced rates of flow in the late summer, since these would result in a decrease in turbidity and thus a marked increase in light availability at the river bed.

'Scouring' and general disturbance of the river bed by turbulence and high rates of flow probably accounts for the presence of many pennate diatoms, which are usually regarded as benthic and attached forms, in the spring and autumn phytoplankton crops. These were particularly noticeable in the spring of 1966 when pennate diatoms represented up to 50% of the total diatom population (see table 4), although for the rest of the period of the investigation, they were only a small fraction of the total. Amongst the most commonly recorded genera were Amphora, Cymbella, Gomphonema, Surirella, Diatoma, Synedra, Navicula and Nitzschia. Although individual species of these genera usually occurred at low concentrations at irregular intervals, some species of the latter

Table 4.     Calculated algal volumes in River Thames samples during 1966-68  
expressed as  $\mu\text{m}^3 \times 10^3 / \text{L.}$  and as percentages.

Date	Week	Total	Total Diatoms	%	Centric Diatoms	%	Crypto- phyceae	%	Chloro- phyceae	%
<u>1966</u>										
Jan. 1	3	288	222	77	108	37	43	15	23	8
Feb. 8	6	127	107	84	57	45	16	12	4	3
Mar. 8	10	170	165	97	62	36	-	-	5	3
Mar.16	11	439	405	92	266	60	20	4	17	4
Apr.13	15	1225	1166	95	916	75	44	4	15	1
Apr.27	17	809	688	85	377	46	86	10	35	4
May 25	21	22559	21789	47	21053	94	363	1	407	2
June 1	22	16302	15878	97	15188	93	178	1	246	1
June22	25	1418	504	35	450	31	141	10	773	54
Aug. 3	31	3951	3290	83	3210	81	232	6	429	11
Aug.31	35	45772	45344	99	45187	98	100		328	1
Sep.14	37	2933	2695	82	2630	80	229	8	409	10
Sep.21	38	2678	2269	84	2242	84	193	7	218	8
Oct.12	40	779	460	59	358	46	78	10	241	31
Nov. 2	44	154	88	57	78	50	45	29	22	14
Nov.16	46	64	35	55	33	51	13	22	15	23

1967

Jan.11	2	53	45	85	29	54	-	-	8	15
Mar. 1	9	1496	1466	98	1460	96	22	1	8	<1
Mar.29	13	2799	2734	98	2680	96	40	1	25	1
Apr.19	16	5436	5383	99	5209	96	33	<1	20	<1
Apr.25	17	22657	22427	95	22082	99	82	>1	148	>1
May 3	18	23783	23371	98	23120	97	343	1	79	1
May 17	20	1947	1846	95	1817	93	37	2	64	3
May 31	22	1428	1242	87	1196	84	68	4	118	9
June14	24	12984	12075	93	11960	92	356	3	553	4
June28	26	6264	6019	96	5996	95	11	<1	234	3
July 5	27	2876	2084	72	2045	71	293	10	499	17

Table 4 (Contd.)

Date	Week	Total	Total Diatoms	%	Centric Diatoms	%	Crypto- phyceae	%	Chloro- phyceae	%
<u>1967 (contd.)</u>										
July 12	28	5659	4268	75	4245	75	386	6	1005	18
July 19	29	2088	1407	68	1384	66	-	-	681	32
Aug. 2	31	1718	950	55	929	54	103	6	665	39
Aug. 16	33	3989	3603	90	3542	88	116	3	270	7
Aug. 30	35	7783	7235	93	7138	91	136	2	412	5
Sep. 5	36	19416	19035	98	18977	98	25	.	356	2
Sep. 20	38	2165	1785	82	1762	81	130	6	250	11
Sep. 27	39	1836	1589	86	1559	85	103	6	144	8
Oct. 11	41	8709	8254	95	8140	94	87	1	368	4
Dec. 13	50	75	57	77	36	48	8	10	10	13
Dec. 27	52	33	29	88	24	72	4	12	-	-
<u>1968</u>										
Jan. 3	1	114	20	17	20	17	94	84	-	-
Jan. 17	3	33	27	82	27	82	6	18	-	-
Feb. 7	6	46	37	80	37	80	9	19	-	-
Feb. 21	8	237	202	85	200	84	24	10	11	5
Mar. 6	10	555	535	96	492	88	8	1	12	2
Mar. 13	11	2013	1950	97	1514	75	38	2	25	1
Mar. 20	12	5923	5773	97	5470	92	82	1	68	1
Apr. 3	14	10870	10770	99	10150	93	44	1	46	1
Apr. 10	15	16112	15880	99	15432	93	128	1	104	1
Apr. 17	16	32890	32799	98	31820	94	58	1	33	1
Apr. 24	17	13662	13517	99	13165	96	145	1	-	-
May 1	18	11593	11352	99	10800	97	241	1	-	-
May 8	19	13900	13732	99	12474	89	176	1	-	-
May 22	21	3272	3168	97	3071	94	106	3	-	-



four genera appeared to have a marked seasonal periodicity.

Diatoma vulgare showed a marked increase in numbers in the spring of 1968 with its maximum at the same time as that of the small centric diatoms, although in the previous years 1966-1967 both this species and D. elongatum had only occurred in low concentration. Although Diatoma was not mentioned by Fritsch (1902-1903) in his survey, Rice (1938) recorded both species as present and suggested that D. vulgare had a single spring maximum with its occurrence corresponding to periods of low flood rainfall and relatively high oxidized nitrogen in the water.

Both Synedra ulna and Synedra acus also showed a distinct spring maximum in each of the three years of this study, at the end of April and the beginning of May. Both species were recorded by Fritsch (1902-1903) and Rice (1938), but they were apparently more abundant. Fritsch summarised the seasonal periodicity of the Thames plankton between Teddington Lock and Kingston as:-

mixed plankton (...with an Asterionella - phase)

Melosira (about May)      Synedra (summer)

mixed plankton (late summer and autumn).

Rice confirmed the summer appearance of Synedra (in particular S. ulna) but considered it to have a larger spring maximum as well. The abundance of these species and other relatively large diatoms in both Fritsch and Rice's surveys may be largely due to the method of sampling by phytoplankton net, which makes comparisons between



their data and that collected during this investigation difficult. However, it is very interesting that the phytoplankton flora in the Thames has not changed drastically in the last 60 years in spite of the marked increase in both agricultural and industrial (urban) pollution.

Although several species of Navicula were observed in the phytoplankton only Navicula ? viridula (cell volume about  $1,390 \mu\text{m}^3$ ) appeared in large concentrations (over 100 cells/ml). In both 1966 and 1968 this species reached a peak just before the small centric diatom vernal maximum, but in 1967 only a few cells were observed at the same time as the main diatom increase. This species was only recorded sporadically throughout the rest of the summer and autumn which is similar to its apparent periodicity in the River Lee (Swale 1964).

Species of Nitzschia, frequently present in the Thames at Walton during this investigation, included Nitzschia acicularis, N. linearis, N. palea, N. sigmoidea and N. ? vermicularis. However, for convenience since they were only observed in small numbers, all the species with the exception of N. acicularis, have been placed together. In estimating their total volume, an average cell volume of  $3,400 \mu\text{m}^3$  was used, and therefore it is very likely that, on occasions, the total volume (~~was over-estimated~~) was over-estimated. The observed periodicity of these species with several small maxima was necessarily rather false, but it was apparent that the main increase

in all of them occurred during the spring and was concurrent with the small centric diatom peak.

The occurrence of N. acicularis was also confined to the spring months when the cell concentrations reached approximately 600/ml in 1967, 870/ml in 1968 and 1720/ml in 1966. Similar concentrations were observed by Swale (1969) in the Rivers Severn and Lee and she considered this species 'to be more truly planktonic than the other pennate species'. Butcher (1932) recorded this species however, as an important member of the attached microflora in several rivers including the Tees.

In the preliminary survey of the Thames between Oxford and Egham in 1968 (see page 123), N. acicularis was recorded at approximately the same concentration (1,000-2,000 cells/ml) throughout this stretch of river, although the small centric diatoms showed marked increase below Abingdon. While definite conclusions can not be made, it does seem likely that either the initial source of this diatom is well upstream of Oxford and that there is little or no growth, except perhaps, sufficient to compensate for any sedimentation or that the main growth occurs throughout the river system while this species is still non-planktonic and benthic, and the observed planktonic stage is mainly the result of a continual cycle of suspension and sedimentation as the water mass moves downstream over new populations.

If this species is to be regarded as truly meroplanktonic, the factors which determine whether or not it becomes planktonic are probably largely unknown, but the presence of a Nitzschia-type plankton in some lakes has been discussed, to some extent, by Richardson in his consideration of diatoms and lake typology in East and Central Africa. (Richardson, 1968),

Asterionella formosa, however, is considered to be an euplanktonic species and therefore probably only survives for short periods on the river bed. It was most commonly recorded in the early spring months, during this investigation, and appeared to reach a maximum at about the same time as the small centric diatoms. For the rest of each year, it occurred in small numbers at irregular intervals, and generally as single cells or broken colonies of two to six cells. Eight-celled colonies were rarely present and the most healthy appeared to be four-celled in size. Swale (1969) also recorded Asterionella formosa in the river Severn regularly, but as occasional cells only. She suggests that difference in sampling technique may account for the relatively higher frequency of this species observed by Rice (1938) in the Thames, and this explanation probably also accounts for the low populations of Asterionella recorded during this study. It seems most likely, in view of the concentration and size of the colonies in the river phytoplankton, that this species is 'tychopotamic' (as defined by

Zimmer 1899 see Fritsch 1902) and is merely carried into the main river system from the outflow of feeder lakes and/or backwaters. Asterionella formosa is often an important member of the spring plankton crops in several reservoirs (see Bellinger, 1968; Gardiner, 1941; Taylor, 1964 and also page 136) and lakes e.g. Virginia Water lake (Evans and McGill in publication) in the vicinity of the River Thames, and thus even the apparent spring maximum in the river may well be due to Asterionella-rich inflows. Neither Fritsch (1902-1903) nor Rice (1938) recorded this species as abundant in backwaters, however.

The presence of Attheya zachariasii in the river during August 1967 may also have resulted from a primary growth in one of the feeder lakes. Although this species has been recorded in the plankton of several American rivers including the Ohio (Lackey, 1943) and the Roanoke (Whitford and Schumacher, 1963), there are apparently very few published reports of its occurrence in the British Isles. Lund (1940) recorded its presence in small shallow ponds and Evans (personal communication) has found Attheya in Virginia Water lake, but it is commonly recorded in many European lakes and Teiling (1953) considered it to be an indicator of eutrophic conditions, together with Fragilaria crotonensis and Melosira granulata, and in the absence of the obviously eutrophic genera such as Microcystis.

Unlike the class Bacillariophyceae, the Chlorophyceae are represented in the Thames flora by genera which have seasonal periodicities mainly confined to the summer and autumn months. This seasonal distribution is reflected in the species composition of the total phytoplankton as this class represents an increasing percentage of this total as the summer progresses (see table 4). A similar pattern of occurrence was reported by Swale (1969) in both the River Severn and Stour as well as the Lee (1964), but it appears that in the Little Miami River (Weber and Moore, 1967) the Chlorophyceae represented a greater percentage of the total river plankton in the winter rather than the summer.

Chlamydomonas was probably the most common Volvocalean genus in the Thames phytoplankton as it was recorded in all the river samples; although during the winter periods, it was only present in very low concentrations. No attempt was made to identify the several different species which were observed, during this investigation, and instead they were grouped together as Chlamydomonas spp. in the phytoplankton counts. The seasonal periodicity of this aggregate is therefore rather misleading and similarly the estimated volumes (based on an arbitrary cell volume of  $300 \mu\text{m}^3$  - see Nauwerck 1963 and Bellinger 1968) may well be inaccurate. However, it was apparent that Chlamydomonas spp. showed a marked spring maximum which coincided with the vernal diatom crop in both 1966 and in 1967, while in 1968, this peak was observed at the same time as the large increase in the very small centric diatom



?Cyclotella sp. (see page 104). These species of Chlamydomonas continued to be very common throughout the summer periods and further maxima were recorded in both 1967 and 1966, but in the latter year these maxima were smaller than the spring increase.

Other Volvocalean genera which were often present in the summer phytoplankton included Carteria, Pteromonas, Phacotus, Haematococcus and Eudorina. However, as they usually occurred in very low concentrations - only a few cells or colonies/ml, regular counts of the individual species in this genera were not made. It seems most likely that these genera were largely derived from the plankton of feeder ponds, shallow lakes and backwaters in the river system, since they are commonly regarded to be typical of such habitats (Hutchinson, 1967).

The greatest proportion of the Chlorophyceae in the Thames flora, as both cell concentration and species composition, belonged to the order Chlorococcales. The most prominent genera included Scenedesmus, Ankistrodesmus and Coelastrum, but at least ten other genera were commonly recorded in the plankton.

A comprehensive species list for Scenedesmus in the Thames and the Thames Valley reservoirs was compiled by Bellinger (1968) during his study of filter beds in this area. The most commonly observed species in the river phytoplankton were S. quadricauda, S. dimorphus and S. acuminatus, but for regular sample counts all the



species were placed together and have been reported in this investigation as Scenedesmus spp.

These species were present in the river throughout the year, although during the winter periods, especially late January and February, only one or two coenobia/ml were recorded. The main increase in Scenedesmus spp. occurred between May and June in both 1966 and 1967, but at the end of May 1968, when regular routine sampling was stopped, this increase had not yet started. In 1966, the maximum number of coenobia was recorded at the end of May, but in the following year the peak was not observed until the end of August. However, in both years these species were very common throughout the summer months until mid-October when there was a marked decrease in numbers. There was no obvious correlation between their periodicity and the nutrient concentration of the river water, and it seems more probable that physical factors of light availability, (perhaps daylength) temperature and turbulence were most influential.

Ankistrodesmus spp. (including A. falcatus and A. falcatus var. spiralis) appeared to have a seasonal periodicity similar to Chlamydomonas spp. although Ankistrodesmus was usually observed in lower cell concentrations. Swale (1969) considered these genera - Chlamydomonas, Scenedesmus and Ankistrodesmus to be the dominant Chlorophyceae in the Severn and Stour, but she recorded them in concentrations which were much greater than any observed in the Thames at Walton. However, it is probable that the concentrations

of these small Chlorophyceae (together with Cryptomonads and small diatoms) are greatly affected by grazing of both the benthic and planktonic fauna. Recent work on the benthic fauna in the Thames at Reading by Mann (1964) and Negus (1966) suggests that this fauna may be extensive although it has been assumed that detritus supplies the main source of food. Swale (1969) reports 'it is significant that mussels in the Thames at Reading increase in size only from mid-April to mid-October (Negus, 1966) after which little phytoplankton would be expected to be available.', and she includes references to several other workers who consider that a high production of benthic animals depends on a large and continual supply of phytoplankton.

Coelastrum microsporum was the other commonly occurring species in the summer of both 1966 and 1967. Although it was occasionally observed in the flora during April 1966, the main increase in the number of coenobia occurred in June to reach a peak at the end of this month. However, in the following year, it did not appear in the phytoplankton until mid-May and it gradually increased to a maximum in mid-July. The species persisted in the plankton until late October while in 1967 it was still present in river samples collected during November. Swale (1964) recorded this species in the River Lee during August, although she did not comment on its occurrence in either the Severn or Stour (see Swale 1969).

Other chlorococcalean genera such as Tetrastrum, Crucigenia, Pediastrum, Dictyosphaerium, Microactinium and Tetraedron did not occur in large concentrations, and other members of the chlorophyceae such as the desmids and conjugates were only occasionally in the plankton.

The Euglenophyceae, especially the genera Euglena and Phacus, were usually present during the spring months at the same time as the increase in the small centric diatoms. but they occurred in low concentrations which made regular counts impracticable.

The Cryptophyceae were the only other class which was regularly represented in the phytoplankton. Rhodomonas minuta var. nannoplanctica and Cryptomonas spp. (including C. ?erosa, C. curvata and C. ?ovata) appeared to have similar periodicities to one another. Although they were present throughout the winter, and occasionally occurred as the dominant organisms in the phytoplankton, they were observed in greater concentrations during the spring and summer months. Maximum numbers of these cryptomonads occurred in May - June in both 1966 and 1968, but in 1967, whilst they also occurred at their maximum concentration during this period, Cryptomonas and Rhodomonas did not reach a maximum at the same time.

Although Cryptomonas ovata was recorded by Rice (1938) in a survey of the Thames phytoplankton, it was apparently not very common, while none of the other species nor Rhodomonas were recorded. Swale had reported the occurrence of Cryptophyceae in several rivers

(see Swale 1964 and 1969 and page 120 of this thesis); and Lund (1962) stated that Rhodomonas minuta var. nannoplanctica, although very common, has rarely been recorded, and admits that there is very little known about its seasonal periodicity or the controlling factors. It seems most likely that grazing and turbulence are of particular importance as factors affecting the population size especially during the summer months, although light availability, temperature and competition from other algae may play an important role in determining the seasonal periodicities of both Rhodomonas and Cryptomonas.

Chrysophyceae did not appear to be very common in the phytoplankton of the Thames at Walton, although both Dinobryon spp. and Synura uvella were observed in the autumn and spring months. A similar pattern of occurrence for this class was observed by Swale in the Stour and Severn and Rice (1938) reported Synura to be common in the plankton but absent during June - August. Mallomonas sp. was only observed on one occasion, in September 1967, in the plankton at Walton, although it appeared to be very common in the plankton sample taken at Oxford in the survey of 1968 (see page 123).

The Cyanophyceae were poorly represented in the Thames flora at Walton and only occasional filaments of Oscillatoria spp. Anabaena sp. and Aphanizomenon flos aquae were observed. It is probable that their presence in the plankton was due to the 'scouring' effect of the current on the river bed and other suitable substrata, although they may have been derived from the plankton of feeder ponds and lakes.



Fritsch (1903) in his paper on the Thames phytoplankton, concluded that 'the Thames had a well-marked living plankton all the year round' and that 'the backwaters, although differing very markedly from the river itself (greater abundance of individuals especially greens and blue-greens) always bear the stamp of a river plankton.' Butcher (1932) considered, however, that in small shallow rivers the plankton represented 'a pale image of the benthos from which it is entirely derived'. There can be no doubt that, from the extensive literature on potamoplankton throughout the world (see Blum 1956), the phytoplankton may be ~~very~~ varied and considerably more abundant than in many lakes. However this does not mean that the opinion of Butcher is completely incorrect, since the benthic and attached microflora, and particularly in the Thames, may be vastly greater in both cell concentration and total volume, than the plankton. Furthermore it is possible that much of the plankton, especially the pennate diatoms, are derived entirely from the benthos. With the possible exception of Asterionella formosa, it is doubtful if all the common species in the Thames phytoplankton at Walton cannot exist as benthos or at least on the river bed for some period of time, and for many this may well be a rich source of potential inoculum. Another source of inoculum is the backwater and feeder ponds and lakes and there have been several reports (e.g. Hartmann and Hynes, 1961; Kofoid, 1902, 1908) and Maciolek, 1967) on the effect of such water bodies on the downstream

potamoplankton. In view of these many sources, it is difficult to decide which species, if any at all, may be considered to be truly potamoplanktonic. It seems not unreasonable that benthic species with planktonic stages e.g. Nitzschia acicularis and perhaps such species as Stephanodiscus hantzschii, which is apparently less common in lake plankton, should be included in this category. If this is so, then Butcher's opinion is quite valid.

A preliminary survey of the Thames phytoplankton at several sampling sites between Oxford and Egham in April 1968.

The regular appearance of small centric diatoms in the phytoplankton of the Thames, for at least the last 30 years, and their continued dominance of the flora for much or all of the growing season prompted speculation on their possible source. Mackenzie (1938) had already considered this, but apart from collecting together much of the available literature on the occurrence of Stephanodiscus hantzschii, did not reach any definite conclusions. Rice (1938) considered this species to be poorly represented in backwaters, although several of the Cyclotella spp. did occur.

Our survey was carried out on the 19th April 1968, two days after the spring maximum had been recorded at Walton. Only eight sampling sites were chosen, as it had been decided that subsequent surveys might be carried out in more detail. Samples of water from



Fig. 14. The variation in the particulate chlorophyll 'a' (●—●) and the concentration of certain phytoplankton at selected sites on the River Thames, between Oxford and Sunbury Lock, on 19.4.68

Rhodomonas minuta ○—...—○

Small centric diatoms ⊙——⊙

Nitzschia acicularis ●——●

FIG. 14

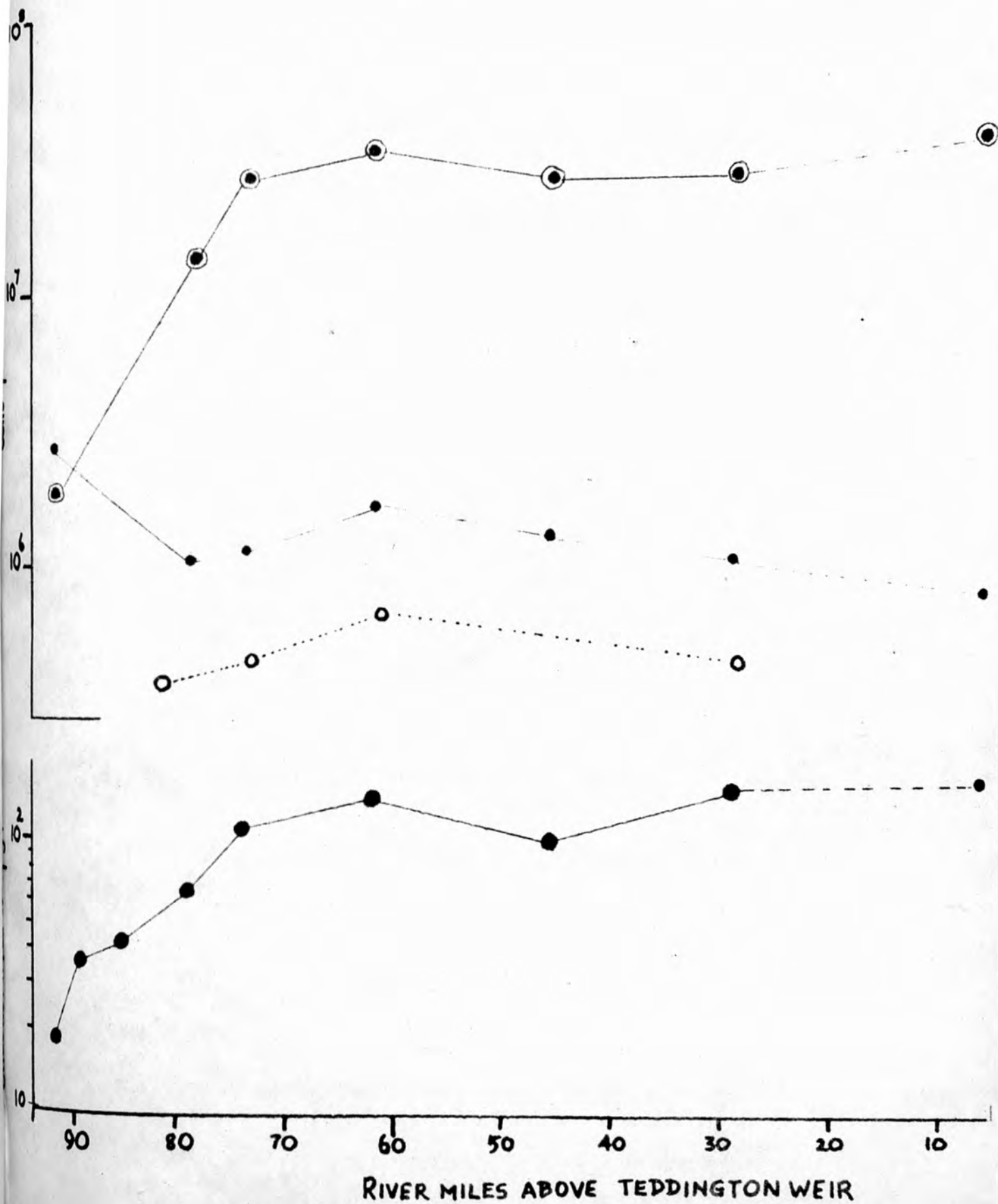
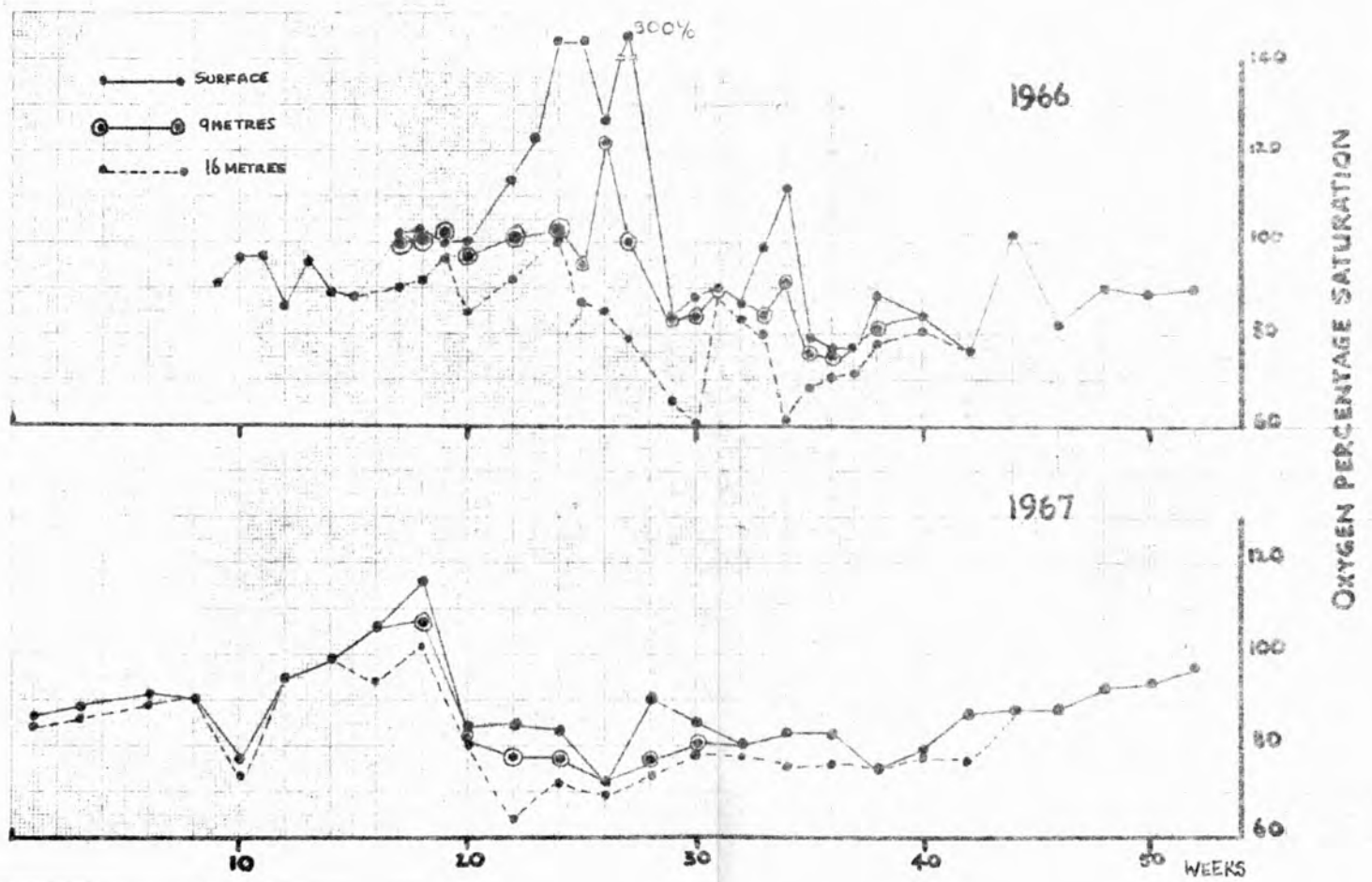


Fig. 15. The seasonal variation in oxygen (expressed as percentage saturation) at the surface, middle (9 metres) and bottom (16 metres) in the Queen Elizabeth II reservoir.

FIG. 15



each site were determined for total chlorophyll content and the dominant organisms were identified. Quantitative counts of only the small centric diatoms, Nitzschia acicularis and Rhodomonas minuta were made with the inverted microscope. The concentrations of these species and the total chlorophyll content are shown in figure 14.

There was a marked increase in the small diatoms between Abingdon and Pangbourne to reach a plateau concentration in the rest of the samples taken downstream. N. acicularis and R. minuta showed little change in concentration along the whole length of the river, but they were considerably smaller populations. The variation in the chlorophyll showed a similar pattern to the fluctuation in the small diatom population.

Although centric diatoms dominated the flora from Abingdon to Egham, other diatoms such as Synedra, Melosira, Diatoma and Navicula were also very common. Chlamydomonas spp. and the cryptomonads, while present in all the samples appeared to be most common in the samples collected in Oxford, Sandford Lock and Abingdon. The phytoplankton population at Oxford was dominated by Chlorophyceae, including Microactinium sp. and Chodatella spp., although both Mallomonas sp. and Euglena spp. were also very prolific. Trachelomonas sp. was common at the Sandford Lock.

Thus the major increase in these small diatoms appeared to occur downstream of Abingdon where the river meanders through rich arable land. The next survey was to have taken place a few days later



in this area, to determine whether or not backwaters were responsible for the increase. However, after a weekend of heavy rain and a week of poor weather, the diatoms were dispersed, and the survey was not possible. In the spring of 1969 a further attempt was made to investigate the occurrence of these small diatoms, but the results have been limited through relatively poor growths (Evans, personal communication). However, the interpretation of data derived from the 1969 extensive sampling programme involving the University of Reading Zoology Department, the Water Research Association, the Metropolitan Water Board, the South West Suburban Water Board and several other Water Companies in the Thames Valley as well as this Department, is in hand. Although this most recent survey is beyond the intended scope of this Thesis it is mentioned here as it is hoped that some of the results of this survey will be published and some points derived from it may appear in discussion in this Thesis.

B. (1). Phytoplankton in the Q.E.II Reservoir

Regular sampling of the phytoplankton in the reservoir was started at the end of November 1965 and continued until May 1968. From January 1966 the phytoplankton in the bulked samples (see page 10) was analysed and the density of the most common species was determined, mainly, in the samples taken at the surface, top (at 1 metre depth), middle (at 9 metres depth) and bottom (at about 16 metres depth) of the reservoir. During periods of marked increase or vertical stratification in the standing crop, the density was determined at intermediate depths, as well. The observed changes in both the plankton density and composition do not necessarily represent the precise fluctuations which occurred within the reservoir. However, for the purposes of comparison in assessing the patterns of phytoplankton succession and their possible relationship with environmental factors, these observed changes are assumed to reflect the general changes in the reservoir.

In spite of the rich assemblage of algal species in the reservoir plankton, fewer than 20 species reached concentrations of  $10^5$  cells (or 'colonies') per litre. In this investigation, only the seasonal periodicity and distribution of these 'major' species have been considered in detail.

Generally the phytoplankton crop appeared to be more or less homogeneously distributed throughout the water column, but occasionally in the summer months, a distinct vertical stratification was recorded

which was not associated with either a marked thermal or chemical gradient. Usually this was due to the concentration of cryptomonads or blue-green algae at the surface of the reservoir and non-motile phytoplankton at lower depths which resulted in the heterogeneous distribution of both the total crop and its component species. An example of such heterogeneity was observed on 19th July 1967. ~~At this time~~ ~~the water was~~ . The cryptomonads and Cyanophyceae - Anabaena circinalis and Aphanizomenon flos-aquae - were ~~also~~ concentrated in the upper three metres of water, whereas the maximum concentration of Tribonema spp. occurred at 5 metres depth and the small centric diatoms appeared to be evenly distributed throughout the water column. A thermal gradient of 1°C difference was recorded between the surface and a depth of 5 metres, but there was no chemical stratification. A possible explanation for this distribution is that the overall turbulence in the column was sufficient to offset the sedimentation of the small centric diatoms but not to prevent the development of a superficial thermal gradient. The cryptomonads, by virtue of their motility, remain in the upper less dense layers, but Tribonema sinks out of these layers rapidly, and appears to accumulate at about 5 metres as its rate of sedimentation is checked by the turbulence. The Cyanophyceae are also sufficiently buoyant to remain near the surface.

A distinct thermal stratification which persisted for several weeks was recorded during June and July 1966 (see page 45) and an increase in the phytoplankton - mainly Fragilaria crotonensis

and Eudorina elegans - in the 'epilimnion' resulted in a marked vertical stratification of the standing crop. ~~(see figure 16)~~ Although such heterogeneity is common in many lakes during the summer months, it was only observed in the reservoir on this one occasion during the period of this investigation.

The seasonal periodicity in the 'major' phytoplankton species in the reservoir was derived from the changes in the mean population density throughout the water column and is shown in figure 16. Where the standing crop was heterogeneously distributed through the reservoir depths, the population density was estimated by planimetry.

#### B. (2). Seasonal Variation in the Phytoplankton in the Reservoir

The major seasonal variations in the standing crop of phytoplankton in the Q.E.II reservoir for the period from January 1966 until May 1968 are shown in figure 16. Although only two complete annual plankton cycles were observed during the period of this study, in neither did the variation in the total crop appear to correspond closely to the conventional conception of vernal and autumn maxima, with summer and winter minima. Hutchinson (1967) in his review of the seasonal succession in freshwater phytoplankton, considered that there were, basically, three types of seasonal cycle - cycles with a single summer maximum; or with two main maxima; or with a complex series of maxima and minima - and it is apparent that

Fig. 16. Seasonal periodicity in some of the dominant and subdominant species of phytoplankton (expressed as numbers of cells per litre) in the Queen Elizabeth II reservoir during 1966 until 1968.

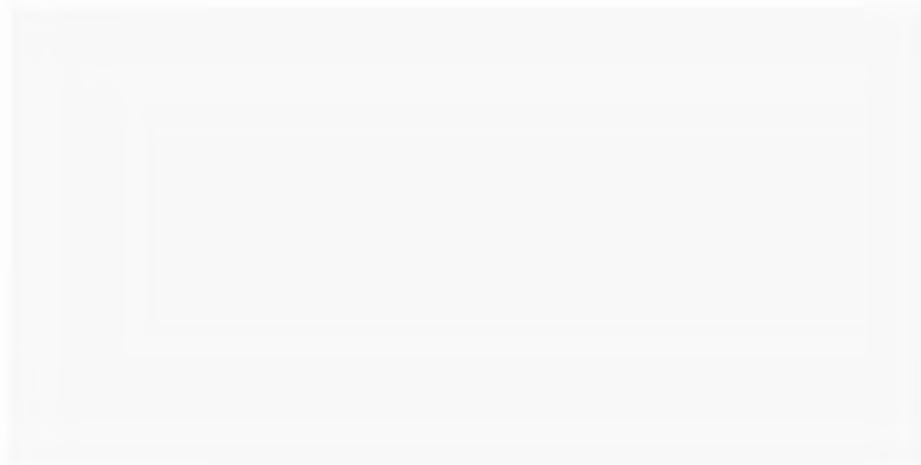
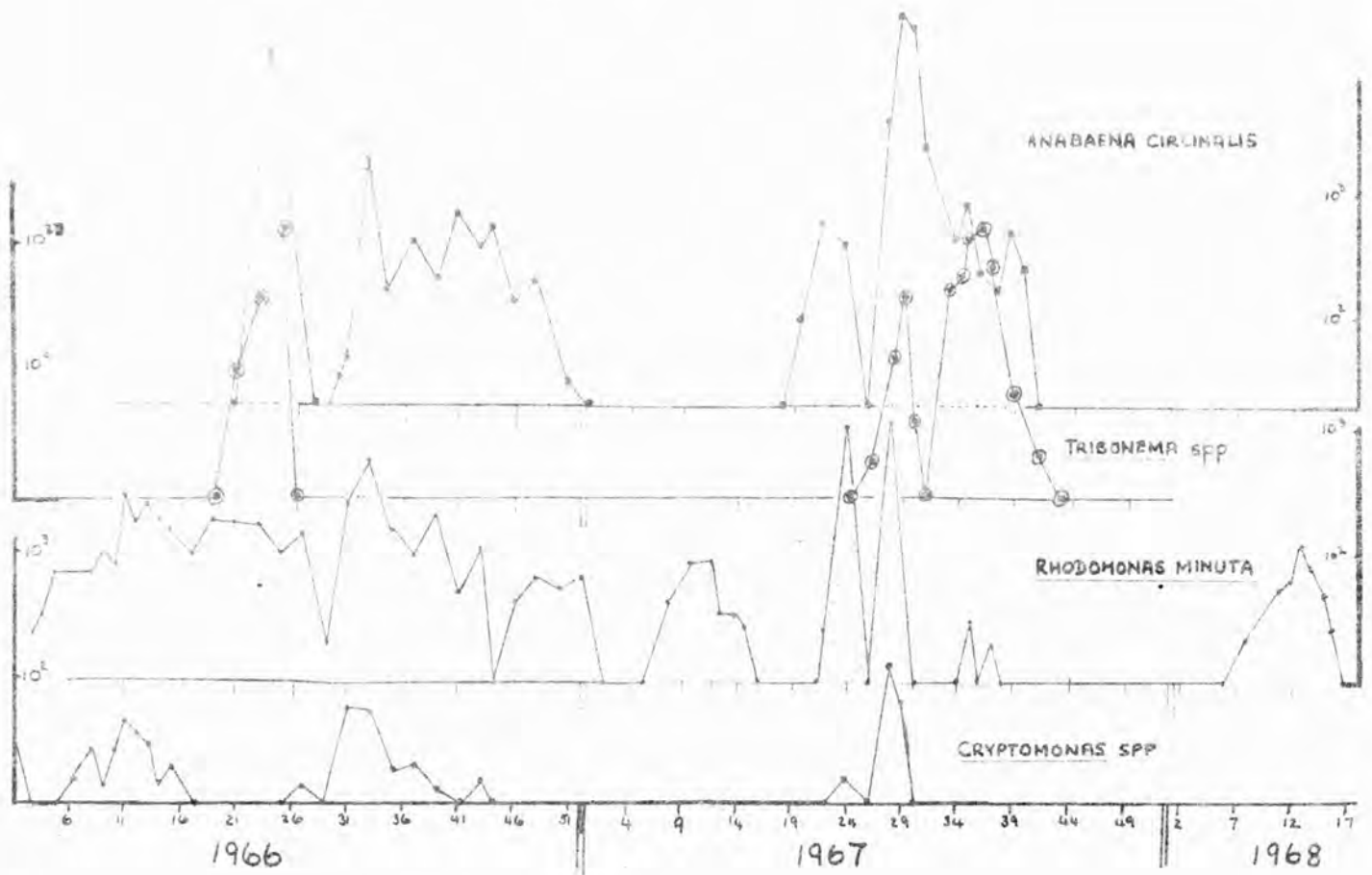
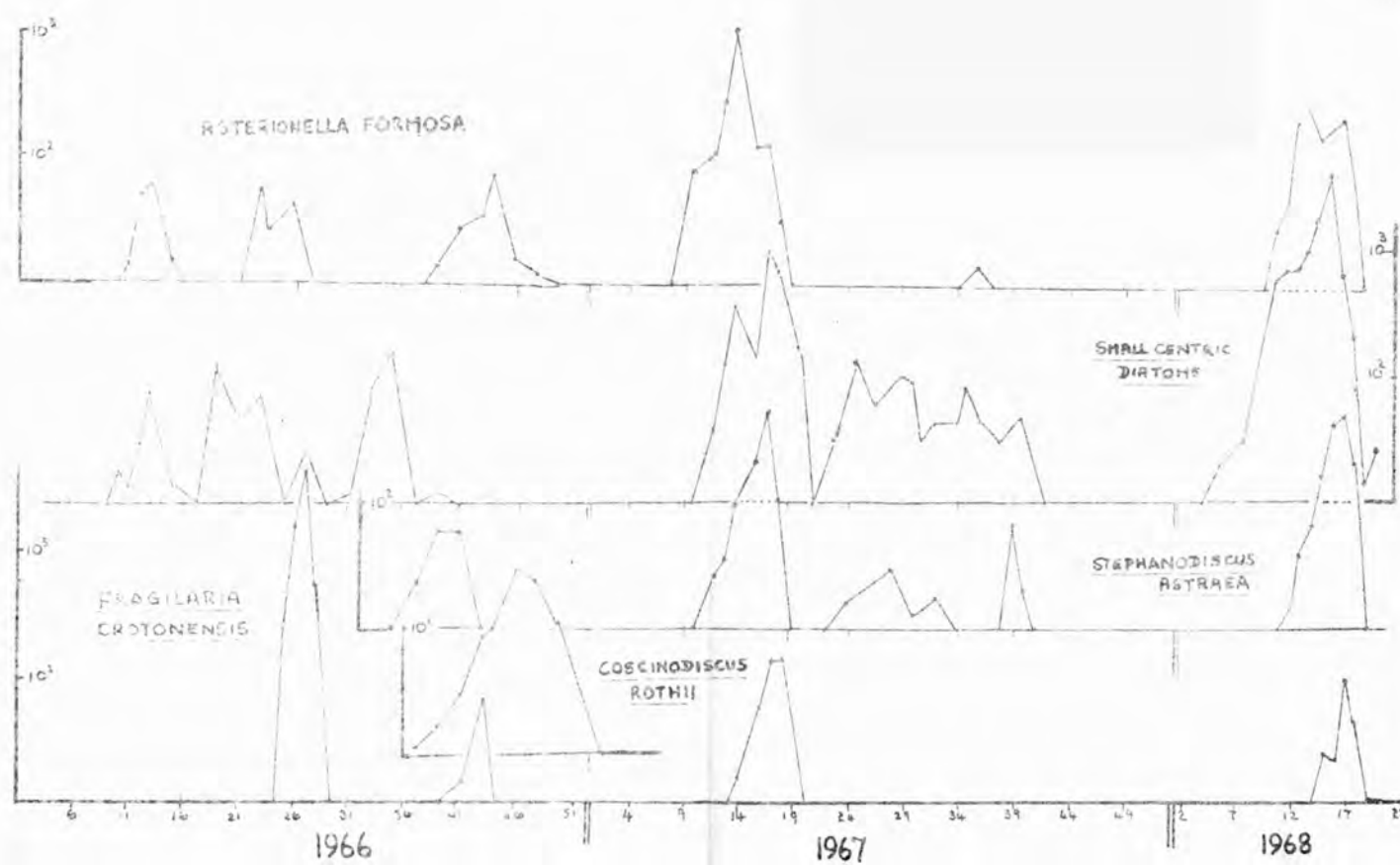


FIG. 16







the annual reservoir cycle resembles this third type, although the spring maximum (in 1967 and in 1968) was more developed than either of the summer maxima . There is however, little information, apart from the work in the Lake District (see Lund 1954) and on Virginia Water lake (Evans unpublished), on the general variation in the seasonal cycle over a period of years. If the overall seasonal pattern is largely determined by environmental factors of turbulence, illumination and thus, nutrients and temperature, the expected variation in the cycle would be small unless there was an associated change in the environment. This appears to be largely correct for these lakes, which are mature. On this basis, it might be assumed that the Q.E.II reservoir, and other reservoirs in which the turbulence may be altered, offer excellent facilities for determining the environmental control of phytoplankton succession, once the basic pattern of the seasonal cycle has been assessed. However, if maturity is considered to be another factor in this respect, then it is possible that the observed annual cycles in the reservoir are transitional stages in the general stabilization of biological conditions (see further on page 159). If this is so, a gradual change to a plankton cycle with spring, late summer and/or autumn maxima which resembles more closely the third type (or possibly the second type) described by Hutchinson may be expected to occur in the reservoir. This type of cycle has been described in other Thames Valley reservoirs (see Bellinger, 1968). Hutchinson (1967) notes the general tendency for

the basic cycle to change from a single maximum to a series of maxima as the lake characteristics alter from large and unproductive to smaller and increasingly more productive. The final pattern to emerge seems to be the monotonous plateau throughout the season as the series of maxima 'merge', which is occasionally found in very shallow, self-regulating systems, e.g. Alderhurst Pond (Evans and McGill in press) and perhaps Lake George in Central East Africa. Thus, this tendency for change could be associated with stability in the ecosystem, and that in an unstable system the cycle becomes a series of maxima which are variable with each season since their development depends entirely on the specific plankton interaction with the variable environment. It seems most probable that the Q.E.II reservoir is such a system and that the annual cycle of succession will remain a variable series of maxima, until it ceases to be a service reservoir. However, by comparison of plankton succession in consecutive years, much information could be derived on the competitive interaction between different species.

In 1966, the plankton cycle consisted of a small peak in May, followed by a large maximum in July and then a gradual increase in the standing crop in the late summer to reach another large maximum in November. In 1967, however, the maximum crop was observed in the spring months and was followed by three smaller summer maxima in June, July and September. There was no obvious winter

maximum in the standing crop and instead the crop density remained low until the spring of 1968.

During the winter 1965-1966 the phytoplankton was dominated, in terms of population density, by Rhodomonas minuta and Cryptomonas spp. although Tribonema spp. persisted in the plankton until the end of January 1966. These cryptomonads increased in number during the spring months, but as co-dominants with the diatoms which did not start to increase until March. Cryptomonas spp. reached a maximum at the end of March and then decreased markedly in April to a minimum in May and June. During July, these species started to increase again to a further population maximum in mid-August which was concentrated in the upper layers of the reservoir and then gradually declined in September and October to the winter minimum. Rhodomonas minuta occurred in much larger numbers than the other cryptomonads and persisted in the plankton during May and June, although there was a decline in the population in April. The summer populations of Rhodomonas were mostly concentrated in the top few metres of water and a maximum of  $1.6 \times 10^6$  cells per litre was recorded in mid-August. In the autumn months there was a gradual decrease in the total population which was more or less homogeneously distributed through the water column, to a minimum in January 1967.

Asterionella formosa and the small centric diatoms, especially Stephanodiscus hantzschii, dominated the spring diatom

flora in 1966, and both populations showed a small but distinct maximum at the end of March at the same time as the cryptomonad maxima. A second, larger spring maximum in the small centric diatom was observed in early May, but in Asterionella this peak was not recorded until June. Similar, but smaller, increases were noticed in several other diatoms including Synedra spp. (S. ulna and S. acus); Nitzschia spp. (including N. acicularis and N. palea) and Stephanodiscus astraea during April and May, but the population densities did not exceed  $2 \times 10^4$  cells per litre.

Slight thermal gradients were observed in the reservoir during May, but the phytoplankton remained homogeneously distributed throughout the water column. However, there was a gradual increase in this gradient throughout June until a  $5^{\circ}\text{C}$  difference between surface and bottom had developed in July and associated with this thermal gradient, there was a marked change in both the phytoplankton distribution and species composition. Tribomena, which was not recorded in the plankton from February until April and only in low concentrations during May, developed rapidly in June to dominate the phytoplankton and reach a population of  $2.8 \times 10^6$  cells per litre in the surface water, near the end of this month. There were possibly several species of Tribonema, occurring together in this population and, for convenience they are referred to Tribonema vulgare agg. in this study. Anabaena circinalis, also recorded sporadically in small quantities in May, developed



into a surface bloom in early June after a week of sunshine, no rain and only light winds. However, it was quickly dispersed within a few days and became subdominant to the Tribonema. A population of Eudorina elegans which started to increase at the beginning of June, also remained subdominant to the Tribonema as its development was checked in mid-June by a severe chytrid infection. A secondary maximum in this species was recorded in early July when a concentration of  $31 \times 10^4$  colonies per litre were observed at 1 metre depth, but it was impossible to establish whether this was due to recovery or the growth of a new resistant strain.

Fragilaria crotensis was only recorded once during the spring increase of diatoms in the reservoir, in phytoplankton counts, although it was usually present in net hauls at this time. However, there was a rapid development of this diatom in mid-June, so that, by the end of this month, it was the dominant species in the phytoplankton. The rapidity with which Fragilaria assumed dominance and the Tribonema population declined suggests that there was a factor of a specific inhibition involved. ( ), although no direct evidence was available. Asterionella formosa and the small centric diatoms were present in the plankton at this time, but it seems likely that the reduction of silica in the upper layers of water was due almost entirely to the increase in Fragilaria. The decrease in other nutrients cannot be so easily attributed to one or more specific phytoplankters. Although it seems most likely that



the dominant organisms were responsible, some 'minor' species, especially the large ones such as Volvox globator, might also have had a considerable effect. This species was observed near the water surface in both June and July, but its maximum concentration did not exceed  $10^4$  colonies per litre, even though many of the colonies were apparently reproducing.

In spite of the presence of at least 10 genera of Chlorophyceae in the reservoir phytoplankton in the summer months, only Shroederia setigera and Eudorina elegans reached concentrations of  $10^5$  cells or colonies per litre. Many of the other genera including Chlamydomonas, Scenedesmus, Ankistrodesmus, and Coelastrum while remaining in low concentrations in the reservoir, were recorded in the river plankton at densities often much greater than  $10^5$  cells per litre.

In mid-July, following a change in the inlet system, the thermal gradient was destroyed and there was a rapid decline in Fragilaria crotensis and the other plankton organisms. The phytoplankton became more or less uniformly distributed in the water column, and Shroederia setigera dominated the standing crop at a concentration of about  $4 \times 10^4$  cells per litre. This species was replaced by the cryptomonads in early August, although there was another increase in Anabaena circinalis at the surface of the reservoir in mid-August. At the end of this month, Stephanodiscus

astraea (cell volume between 3,000 and 4,000  $\mu\text{m}^3$ ) which had been present in the phytoplankton since mid-June, reached a mean population density of  $6 \times 10^5$  cells per litre to co-dominate with the cryptomonads and Anabaena circinalis. However, no apparent decrease in the silica content of the water was observed at this time, even though S. astraea dominated the plankton in terms of biomass. By mid-September, there was a marked decline in the Stephanodiscus astraea population, although it persisted in the plankton until October, and occasional cells were recorded throughout the winter period.

In September 1966, a large centric diatom referred to Coscinodiscus rothii Grun. (?Actinocyclus sp.) appeared in the plankton. This species had not been previously recorded in any of the Thames Valley reservoirs and neither Fritsch (1902-1903) nor Rice (1938) reported its presence in the River Thames flora. It seems most likely that this species was derived from an inoculum of cells in the sediments at the bottom of the reservoir (see pages 186-7) although its original source must have been the river. There was a gradual increase in this species throughout the autumn until mid-November, when the mean population density in the reservoir reached  $3 \times 10^5$  cells per litre.

Although Coscinodiscus rothii dominated the phytoplankton from September 1966, until January 1967, smaller maxima were observed in both Fragilaria crotensis and Asterionella formosa in

October and early November. In spite of this diatom increase, the silica concentration apparently decreased very slightly throughout this period, and a marked increase in the oxygen content of the water only occurred in early November (see pages 91-9). The population of Fragilaria declined rapidly in mid-November but Asterionella formosa persisted in small numbers throughout the winter period, to become co-dominant with the cryptomonads and the small centric diatoms, when Coscinodiscus eventually disappeared from the plankton at the end of January 1967.

At the end of February, there was a marked increase in the number of both Asterionella formosa and Rhodomonas minuta, but Cryptomonas spp. remained in low concentrations throughout the spring period. Rhodomonas minuta reached a maximum concentration at the end of March, but then decreased to minimal numbers during April and May. Asterionella formosa, however, continued to increase, throughout March, while Stephanodiscus astraea and the small centric diatoms were only just starting to increase. Although these ~~three~~ diatoms, dominated the vernal phytoplankton crop, their maxima occurred separately so that both genera assumed total dominance (in terms of population density) for a short period. Asterionella formosa reached a maximum in early April with a mean population density of  $1.1 \times 10^6$  cells/litre, but it had decreased considerably by the end of this month, when the centric diatom maxima were recorded. The mean concentration of S. astraea (cell volume between 13,000 and 16,000  $\mu\text{m}^3$ ) reached  $5 \times 10^5$  cells/litre, while

the small centric diatoms population increased to a mean density of  $4 \times 10^6$  cells per litre. Although there was a rapid decline in both populations, the small centric diatoms persisted in the plankton until mid-May as co-dominants with a small population of Fragilaria crotonensis, which had reached a maximum at the beginning of May. Although the vernal diatom crop was associated with a marked, but gradual decrease in silica during April, oxygen supersaturation in the water was only recorded at the end of the month. At this time, the silica concentration was probably approaching a limiting concentration. Small populations of diatoms persisted in summer plankton, but usually as minor constituents.

At the end of May there was a marked increase in Anabaena circinalis in the surface waters, and apparently closely associated with it, an increase in Chlamydomonas spp. However, no direct evidence of their interdependence was available as all attempts to culture these species failed. It is possible however, that Chlamydomonas spp. were stimulated by the liberation of organic extracellular substances by the Anabaena (see both Fogg and Syrett in Lewin, 1962). Anabaena circinalis continued to form small surface blooms throughout the summer months, but it reached a maximum concentration of approximately  $35 \times 10^6$  cells per litre in the top metre of water in mid-July. Although this species always dominated the blooms of Cyanophyceae in the reservoir, Aphanizomenon flos-aquae and more rarely Microcystis sp. were present in small quantities.

After spring minima in April and May, the cryptomonads increased rapidly in June and continued to show marked fluctuations in population density, particularly in the surface waters, in both July and August. In mid-June and again in mid-July, Rhodomonas minuta reached concentrations of  $2 \times 10^6$  cells/litre, while Cryptomonas spp. present as a much smaller population, reached  $2 \times 10^5$  cells/litre.

Although the summer phytoplankton was predominantly chlorophycean in composition, most of the individual species remained in low concentrations. Pediastrum, Coelastrum and Scenedesmus showed obvious increases in population density but did not exceed  $10^4$  coenobia per litre. Shroederia setigera reached a concentration of  $10^5$  cells/litre during early June, but it had decreased considerably by the end of this month, and persisted in low concentrations for the rest of the summer. Eudorina elegans although co-dominant in July phytoplankton, in 1966, did not occur in large concentrations during 1967. A gradual increase in Tribonema vulgare agg. during June and July was checked, as much of the population became infected with chytrids. However after a marked reduction during August, this alga eventually reached a mean population density of  $1.5 \times 10^6$  cells per litre, in mid-September as the dominant member of the phytoplankton. By the end of this month, Tribonema had decreased considerably but it persisted in the plankton until late October.



The autumnal crop of diatoms was much smaller than either that recorded in the autumn of 1966, or the spring growth in 1967. The small centric diatoms, after an initial summer increase in June, gradually decreased in number throughout the summer, and autumn, to a population density of less than  $10^4$  cells per litre in mid-October. However, the population of Stephanodiscus astraea, consisting mainly of cells of smaller diameter (~~smaller~~) showed two distinct maxima during July and early October. Although this autumn maximum was greater than that in July, on neither occasion did the population density exceed  $10^5$  cells/litre. Neither Asterionella formosa nor Coscinodiscus rothii though present in the autumn phytoplankton reached population densities greater than  $10^4$  cells/litre.

During the winter of 1967 and 1968, the standing crop of phytoplankton was very small, and as in the previous winter 1965-1966 dominated by cryptomonads and small centric diatoms. These algae started to increase during early February, and by mid-March, the small centric diatoms dominated the flora. During the same month, there was gradual increase in Asterionella formosa until it reached a maximum population of  $2 \times 10^5$  cells/litre in early April. However this species remained sub-dominant to the small centric diatoms which had increased by this time to  $10^6$  cells/litre, although their maximum population was not recorded until mid-April at a density of  $4.8 \times 10^6$  cells/litre. Large cells ~~which~~ of



Stephanodiscus astraea, did not start to increase in number until the end of March, but by the end of April, the species was co-dominant with both Asterionella and the small centric diatoms and it reached a maximum concentration of  $5 \times 10^5$  cells per litre. By this time, the silica concentration in the reservoir had decreased to 3.4 mg/l, which would have probably limited any further increase in this large centric diatom (see page 168). Although these ~~diatoms~~ diatoms dominated the spring flora in 1968, the population densities of both Fragilaria crotensis and Nitzschia acicularis reached  $10^5$  cells/litre. The Nitzschia maximum was recorded at the same time as the small centric diatom peak, while the Fragilaria maximum was coincidental with that of the larger Stephanodiscus. Smaller population increases during the spring were noted in Synedra acus and S. ulna, Diatoma vulgare, and D. elongatum and Melosira varians, but the cryptomonads decreased rapidly in concentration after reaching an early maximum at the end of March. A similar decrease in population density was observed in Chlamydomonas spp. and Ankistrodesmus spp. after these species had started to increase rapidly in early April.

The diatom crop, declined rapidly in size during early May and at the end of May, when routine phytoplankton sampling was stopped, the standing crop was very small.

IV. B.

3. The particulate seston and the phytoplankton standing crop in the River Thames at Walton and the Q.E.II reservoir during 1966-68.

Although the estimation of phytoplankton 'biomass' and standing crop are fundamental requirements for an understanding of the reactions of the phytoplankton to their environment, there is no general agreement as to the best methods of estimation or even, the criterion to use (Westlake 1965). Until these difficulties are resolved, the total phytoplankton crop is best described by several parameters, including those which, strictly, measure particulate seston. During this investigation, the 'chlorophyll a', dichromate-oxidisable carbon, dry weight and ash free dry weight of the particulate seston were determined in addition to the volume of the standing crop of phytoplankton. The seasonal variation in these quantities for the river and the reservoir (representing the weekly mean for the whole reservoir) is shown in figs 17 and 18 A. & see 18 B p. 149

The standing crop was determined by the addition of the population densities of the individual 'major' species of phytoplankton. Thus, although this standing crop does not represent the total phytoplankton population, it has been assumed that it does approach the total 'biomass'. The population density for each of the 'major' species was calculated as the product of the cell concentration and the mean cell volume. These volumes were derived from the linear

dimensions of the cells and their approximation to simple geometric shapes (personal observations and Bellinger 1968). Since there was a marked, often seasonal, variation in the mean cell volume in several species (see Bellinger 1968), it was usually necessary to take a mean value in estimating the crop size. ~~and these values were~~  
~~given in table 1.~~

The observed standing crop of phytoplankton in the river ranged from  $0.05 \text{ mm}^3$  -  $45 \text{ mm}^3$  per litre, but the mean annual crop size appeared to be similar in each of the three years of this investigation.

<u>Year</u>	<u>No. of samples.</u>	<u>Annual mean crop.</u>
1966	15	$7.2 \text{ mm}^3$ per litre
1967	20	$6.7 \text{ mm}^3$ " "
1968	14	$7.6 \text{ mm}^3$ " "

Although this mean crop is, perhaps unexpectedly, low in view of the eutrophic nature of the river, it probably reflects the overriding importance of factors such as high turbulent flow and perhaps much reduced illumination. While it is probably impossible to estimate with any accuracy, the upper limit of phytoplankton production in the river, it seems likely that this limit for diatom production may be between  $40 - 60 \text{ mm}^3$  per litre. This estimate is based on the marked decrease in the silica concentration in the river (approaching a limiting value), associated with the spring

diatom crops. ~~(see page 148)~~ The maximum crop observed in the river however, was recorded in the late summer 1966. This diatom crop, composed largely of Stephanodiscus astraea (mean cell volume  $4000 \mu\text{m}^3$ ), appeared to be exceptional since the silica concentration recorded concurrently in the river was 5 mg/litre, although there was an overall decrease of at least 7.0 mg/l associated with this crop. However the calculated silica requirement for this crop was either 9 or 18 mg per litre, assuming that the specific gravity of frustule silica is either 2.07 or nearer 3.9 (see page 144). If the former estimate is correct, the silica concentration was approaching a limiting value and the total crop would not have exceeded  $70 \text{ mm}^3$  per litre which is close to the estimated limit of diatom production. If the crop requirement was closer to 18 mg of silica per litre, it seems likely that, unless there was a rapid replenishment of silica from the bottom deposits, the diatom crop was allochthonous and largely inactive. If this was so, it is probable that the production limit may be closer to  $40 \text{ mm}^3$  per litre.

Stephanodiscus astraea - calculation of theoretical silica requirement during the summer of 1966.

Calculated cell volume =  $4,000 \mu\text{m}^3$

Frustule volume, as percentage of total cell volume = 10%

(see page 168)

$\therefore$  Frustule volume =  $400 \mu\text{m}^3$

(a) Assuming that the specific gravity of silica in

Stephanodiscus astraea is 3.9 (see page 168)

1 cell contains  $400 \times 3.9 \times 10^{-6} \mu\text{g. Si.}$

$\therefore 2.5 \times 10^5 \text{ cells} = 1 \text{ mm}^3 \text{ crop volume}$

$= 4.0 \times 10^2 \mu\text{g. Si.}$

$\therefore \frac{45 \text{ mm}^3 \text{ cell volume}}{K} \overset{\text{requires}}{K} 18 \text{ mg Silica}$

(b) Assuming that the specific gravity of silica is 2.07 (see Lewin 1953)

1 cell contains  $0.8 \times 10^{-3} \mu\text{g Silica}$

$\therefore 2.5 \times 10^5 \text{ cells} = 1 \text{ mm}^3 \text{ crop}$

contains  $2.0 \times 10^2 \mu\text{g Silica}$

$\therefore \frac{45 \text{ mm}^3 \text{ cell volume}}{K} \text{ requires } 9.0 \text{ mg silica}$

There was a close association between the calculated phytoplankton crop and the seasonal variation in the 'chlorophyll a' in the particulate seston in the river, (~~81g~~). The concentration ranged from  $2.4 \text{ mg/m}^3$  to  $175 \text{ mg/m}^3$  in the river, with minimum levels during the winter period. The maximum concentration of  $171\text{-}175 \text{ mg/m}^3$  was recorded on two occasions - June 1967 and in April 1968 - but the concentration of chlorophyll per  $\text{mm}^3$  of algal crop was not the same. In June 1967 there was approximately  $26.0 \text{ } \mu\text{g}$  per  $\text{mm}^3$  of algal crop whereas in the spring 1968, this had decreased to  $5.15 \text{ } \mu\text{g}$ . This variation in the apparent chlorophyll content of the phytoplankton crop, was not limited to these crops, but occurred throughout the period of investigation, and some values for the summer crops of phytoplankton in the river are shown in table 5. Although it is generally considered that there is no constancy between cell volume and chlorophyll content (see for example Mullin, Sloan and Eppley 1966) it seems probable that the variation observed in the river during the summer months reflects the variation in the species composition and the diversity of the phytoplankton crop rather than any nutrient (particularly nitrogen deficiency) limitation. The lower values - under  $10 \text{ } \mu\text{g}$  chlorophyll per  $\text{mm}^3$  algal volume - appear to be associated with crops consisting predominantly of diatoms, whereas the higher values are mostly associated with crops in which there is a large proportion of green algae. Talling (1966), with reference to other works suggests that



Table 5.

Chlorophyll content ( $\mu\text{g}$  per  $\text{mm}^3$  algal volume) of  
phytoplankton crops in the River Thames

Date	Calculated algal volume	Observed chlorophyll	Chlorophyll $\mu\text{g}/\text{mm}^3$ algal crop	
5.9.67	19.42 $\text{mm}^3$	100.87 $\mu\text{g}$	5.2 )	
30.8.67	7.78 "	74.4 "	9.55 )	predominantly diatoms
16.8.67	3.98 "	35.8 "	9.0 )	
14.6.67	13.39 "	111.0 "	8.25 )	
21.6.67	6.26 "	171.0 "	26.2 )	diatoms with greens
5.7.67	2.88 "	61.6 "	21.4 )	
31.5.67	1.43 "	18.0 "	12.5 )	
13.3.68	2.01 "	15.55 "	9.2 )	predominantly diatoms
20.3.68	5.92 "	62.9 "	10.6 )	
3.4.68	10.87 "	74.0 "	6.8 )	
10.4.68	16.11 "	123.0 "	7.7 )	
17.4.68	32.9 "	175.0 "	5.15 )	
24.4.68	13.66 "	134.9 "	9.9 )	
1.5.68	11.6 "	138.7 "	11.9 )	

Table 5 (contd.)

Chlorophyll content of some natural populations of algae in the

Q.E.II Reservoir

Species	Date and Depth	Total Calculated Volume /L	Chlorophyll /L	Chlorophyll content /mm <sup>3</sup> calculated algal volume
Mixed Spring Diatoms (mainly Centrales)	Spring 1968 Average " " " "	3.8 8.05 7.45	26.8 44.4 38.7	7.05 µg/mm <sup>3</sup> 5.5 " 5.2 "
<u>Anabaena circularis</u>	19.7.67 Surface  26.7.69 Surface	1.09 mm <sup>3</sup> (other spp. less than 20%) 0.945 mm <sup>3</sup>	9.01 µg  6.7 µg	8.25 µg/mm <sup>3</sup>  7.1 µg/mm <sup>3</sup>
<u>Tribonema</u>	At surface At 1 M At 1 M	1.18 1.31 3.17	8.2 µg 13.6 µg 27.2 µg	6.9 µg/mm <sup>3</sup> 10.4 " 8.6 "

'much higher contents may occur in green algae'. Although the chlorophyll content per algal biomass in the river compares closely with the values quoted by Krey (1957), they are considerably higher than the mean value suggested by Wright (1959). There is, however, the possibility that some of the chlorophyll is associated with detrital matter (Gillbricht 1952, Harvey 1950) and the values in the river are overestimates of the real algal chlorophyll content. This possibility is discussed more fully in connection with the chlorophyll measurements in the reservoir.

In addition to chlorophyll a, some more generalised information was obtained from the pigment extracts by comparing their absorption at the wavelengths 4500 Å and 6650 Å. This ratio is considered to give an approximate indication of the ratio of 'carotenoids' to 'chlorophyll a'. Other ratios to indicate the same pigment ratio have been used by other workers (see Talling 1966 and Margarlef 1965). Margarlef (1965) considered that this ratio was useful as a measure of 'community structure' as well as an indication to the physiological status (with respect to nutrients) of the phytoplankton. However, in the presence of large amounts of detritus, this ratio may indicate the quantity of degraded chlorophyll and the more resistant carotenoids rather than anything else. The variation in this ratio  $O.D._{450}$  to  $O.D._{665}$  in pigment extracts from some algae, in unialgal but not axenic cultures, are given in table 6. Although there was a large range in values, the maximum value (obtained in a culture of Euglena gracilis) did not exceed 3.02 while the minimum, 1.03, was considerably greater than

Table 6

"Carotenoid to chlorophyll" ratios in some algae

Algae	No. of Samples	OD450 : OD665 ratio
Scenedesmus <sup>0</sup>	2	1.48 - 1.8
Chlamydomonas ? <sup>g</sup> leocystiforme	4	1.8 - 2.64
Chlamydomonas sp.	1	2.42
Eudorina elegans	1	1.03
<sup>um</sup> Cosmaria botrytis	3	1.34 - 1.57
Euglena gracilis	1	3.02
Tribonema ? vulgare	6	1.08 - 2.32
Anabaena inequalis	2	1.34 - 1.47
Natural bloom Microcystis/ Anabaena	1	2.26
Stephanodiscus astraes (net haul)	1	2.62
Asterionella formosa	4	1.95 - 2.95
Navicula species	3	2.3 - 2.89
Fragilaria crotonensis	1	1.65
Melosira varians	1	
Mixed diatoms (net haul)	1	2.2

the estimated value of 0.35 for pure chlorophyll a from Nettle leaves. In the river, this ratio ranged from 1.58 to 3.64, with the maximum values generally occurring during the winter period. The seasonal variation in the pigment ratio is compared with the variation in chlorophyll a in the river in fig 21A. While the ratio value did not vary much during June and July 1966, there was a marked increase in value during August which probably reflects the increase in the diatoms in the river at this time. However, it is unlikely that this change was due entirely to plankton diversity, since, after a marked decrease in the middle of September (weeks 36-37) the ratio remained low throughout the diatom increase in early October and also during the spring increase in 1968. There is some evidence that in certain organisms, including algae, there is an increase in the carotenoid/chlorophyll ratio in response to high illumination (see Wolken and Mellon 1956, Talling 1966), and in view of the low river flow and high solar radiation levels during August, it seems likely that the high ratios recorded in this month may have been due, in part, to the phytoplankton response to this high illumination. Similarly, the low ratios in October 1967 and later in the spring 1968, reflect an algal response to low illumination. The generally high ratios observed in the winter period are most probably the result of non-degraded carotenoids and chlorophyll degradation products in the detritus, and do not

specifically reflect conditions in the phytoplankton crop.

Close correlations between the other parameters of the particulate seston and the standing crop of phytoplankton in the river were usually masked by the presence of detrital matter. The total dry weight of particulate matter in the river ranged from 1.03 mg to 98 mg per litre with the highest values usually associated with marked or prolonged high river flows. These values indicate, perhaps, the general disturbance of bottom deposits as well as allochthonous material introduced from the catchment area. There were marked increases in the sestonic dry weight associated with the maximum increases in the phytoplankton crops in the river but usually, on these occasions the dry weight did not exceed 30 mg per litre. The ash-free dry weight (organic matter) of the seston was also very variable, ranging from 20% to 80% of the dry weight with a mean value of approximately 50%. This mean value is considerably higher than that suggested by Weber and Moore (1967) for the seston in the Little Miami River, although the actual range of ash free dry weight is apparently similar in both rivers. They considered that most of the organic matter in the Little Miami river in the winter months was allochthonous or scoured from the river bed, while in the summer, the organic matter was largely autochthonous. It seems likely that this is also true of the sestonic organic matter in the river Thames. The 'oxidisable' carbon content of the particulate seston in the river averaged between 10% and 20% of the total dry weight and about 30% of the



organic matter which suggests that much of the sestonic organic matter may have been composed of complex polysaccharides and non-planktonic in origin. Marked increases in the percentage of oxidizable carbon in the organic matter associated with large phytoplankton crops, supports this hypothesis.

The relationship between the chlorophyll a and oxidisable carbon contents of the particulate matter is shown in fig 18 and indicates an approximate chlorophyll to carbon mean ratio of 1:400 which is ~~close to~~ <sup>lower than</sup> the ~~maximum~~ <sup>minimum</sup> determined by Steele and Baird (1961) in the North Sea seston. However, this ratio is variable with the maximum values associated with the peak crop production and the minima in the winter and often immediately following the peak production.

The range of the size of the standing crop in the Q.E.II reservoir was considerably smaller than that observed in the river and in other Thames Valley storage reservoirs (see Bellinger 1968). The maximum crops (approximately  $8.0 \text{ mm}^3$  per litre) were observed in the spring of 1967 and 1968 and consisted of diatoms of both allochthonous (river) and authchthonous derivation (see page 182). The crops of authchthonous derivation were smaller, the maximum reaching about  $5.0 \text{ mm}^3$  per litre was composed of Fragilaria crotensis in the summer (see page 133) and of Coscinodiscus rothii in the winter of 1966. Although there is some evidence to suggest that crop production is affected by the 'age' of the reservoir (see page 158)

Fig. 17. Seasonal changes in calculated algal volumes (C.A.V.) (unbroken line), total particulate volumes (T.P.V.) (broken line), Carbon (C) (unbroken line) and dry weight of suspended matter (DW) (dotted line) in the Queen Elizabeth II reservoir during 1966 and 1967.

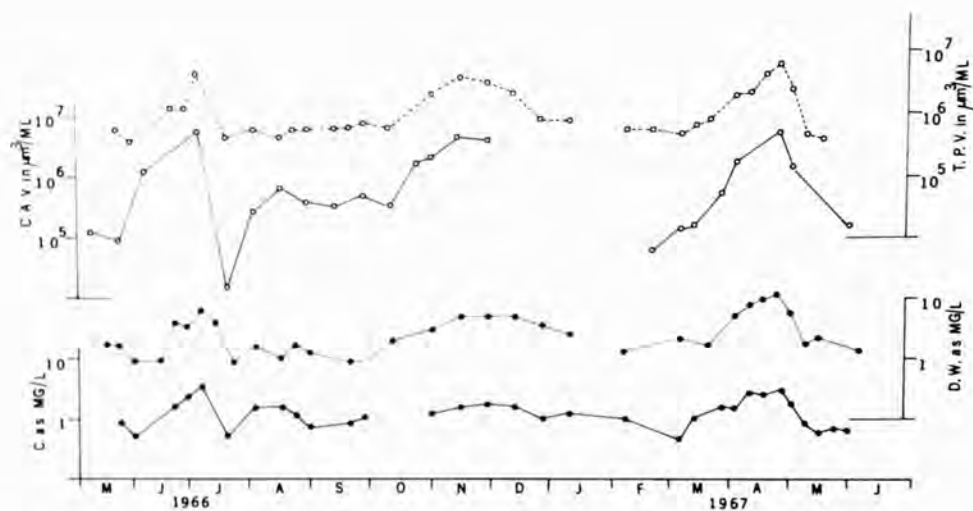


Fig. 18. (a) Seasonal variation in the total particulate volume (T.P.V.) (•——•); chlorophyll 'a' (⊙——⊙); carbon (•-----•); total dry weight ( +----+ ), and ash weight (○——○) in the River Thames during 1967 and 1968.

FIG. 18 A

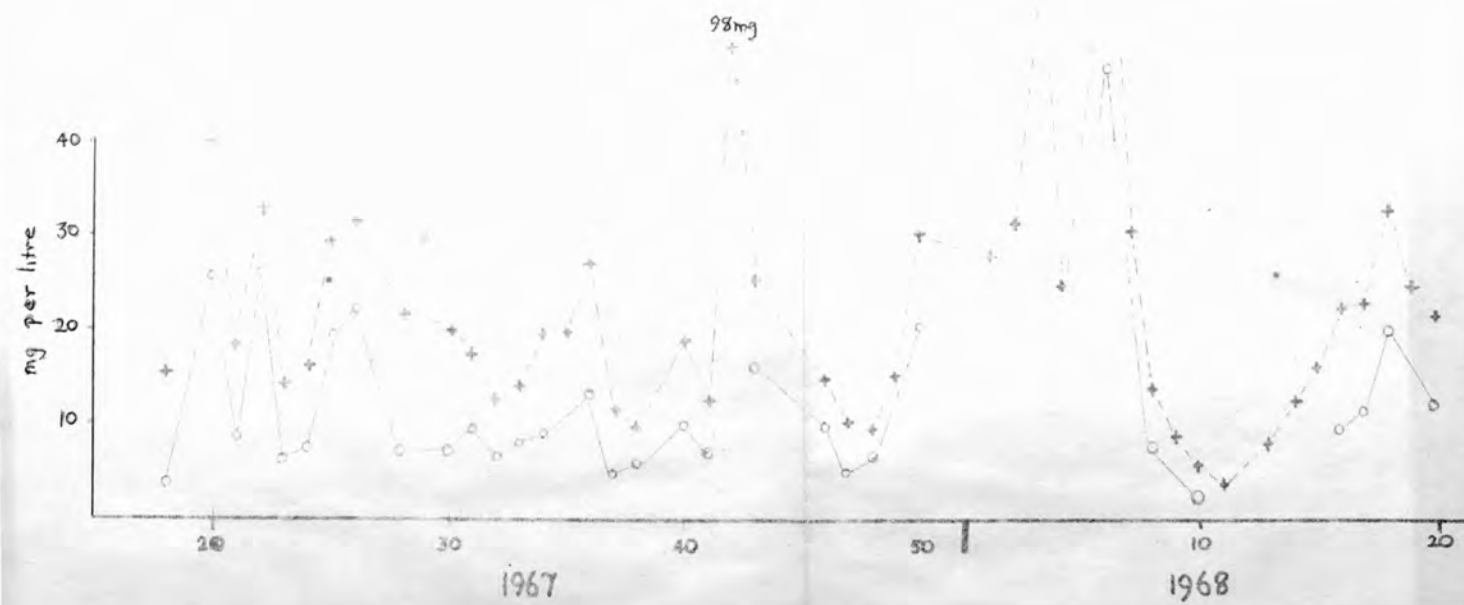
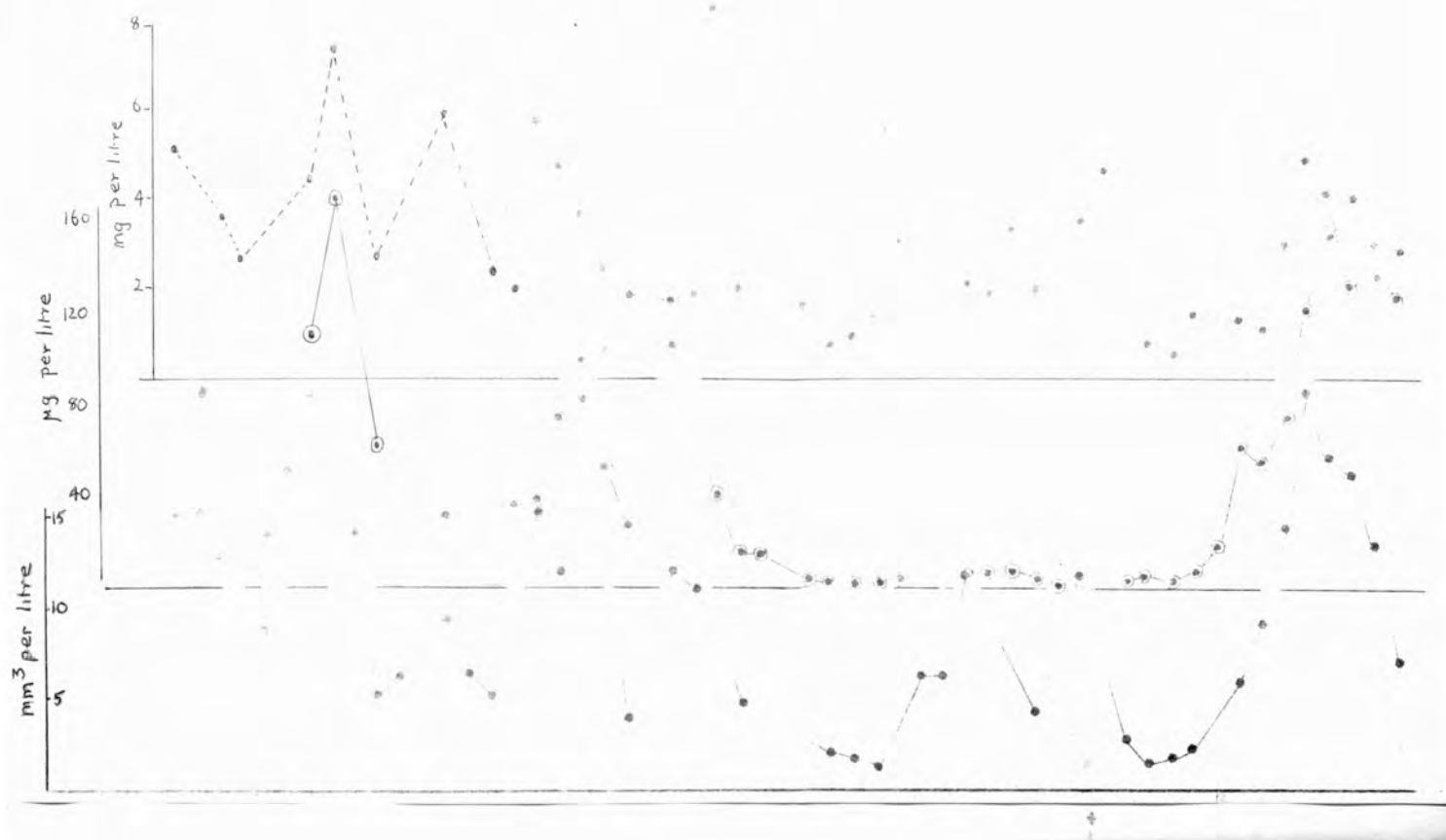


Fig. 18 (b).     A comparison of the total particulate volume  
and chlorophyll 'a' (1);    calculated algal  
volume (2) in the River Thames in 1966 - 1968.

FIG. 18 B

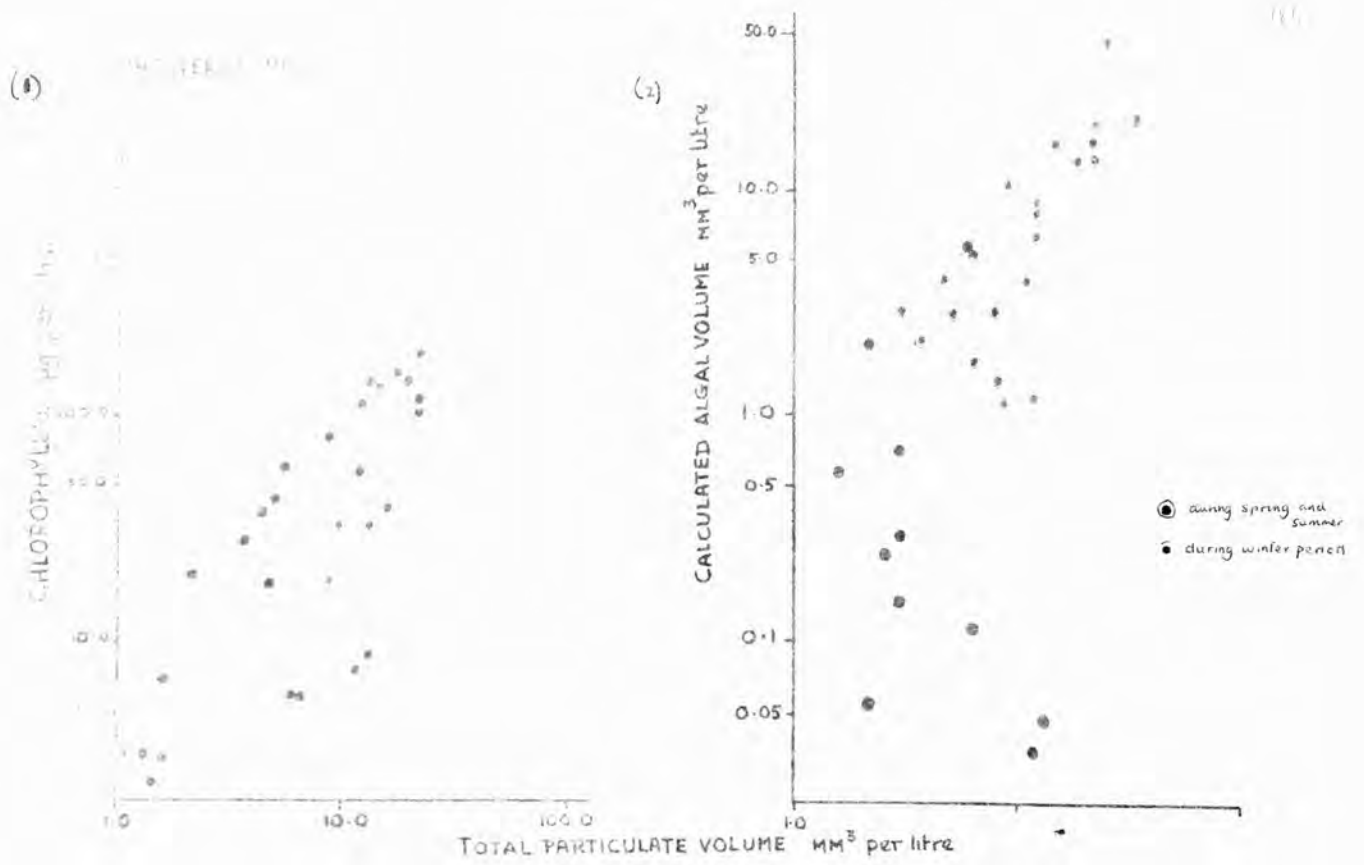
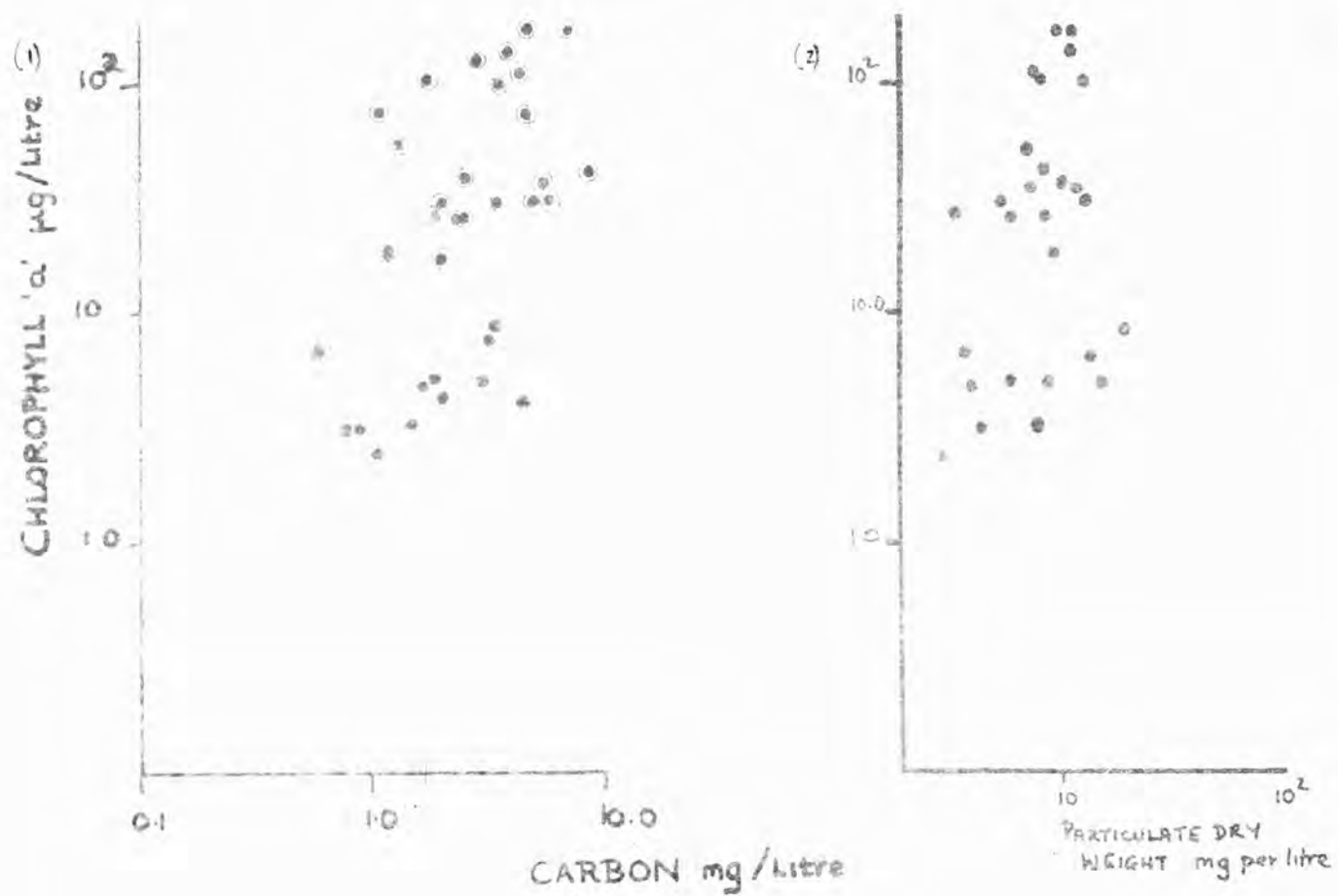




Fig. 18 (c).     A comparison of the chlorophyll 'a' and  
carbon (1), and particulate dry weight (2)  
in the River Thames in 1966 - 1968.

FIG. 18C



it seems probable that, as in the river, the continual throughput of water and turbulence may be of overriding importance in this respect. A similar conclusion was reached by Brook and Woodward (1956) in their study of plankton in small lakes.

The seasonal variation in the chlorophyll a concentration at the surface, 9 metres and near the bottom of the reservoir is shown in fig 203. Since the standing crop of phytoplankton and thus the chlorophyll a was largely evenly distributed through the depths the variation at the other depths have not been included in this figure, except to indicate the superficial crop of Anabaena circinalis in July 1967 and low surface concentration of diatoms in the spring 1968. The maximum concentrations in chlorophyll a were recorded in the reservoir at the time of the spring diatom increases, but the highest quantities of pigment per  $\text{mm}^3$  of algal biomass were found in the summer and winter phytoplankton crops. The summer crops were composed of non-diatomaceous plankton mainly, which would normally have higher chlorophyll contents, while the high winter pigment/biomass ratios may be due either to the response to low illumination by the algal population or the presence of large amounts of detrital chlorophyll. Although there is no direct evidence of such chlorophyll in the reservoir, a statistical regression of oxidisable carbon content on the chlorophyll content of the seston in the

reservoir from November 1967 until March 1968, indicated that there was not a linear relationship between these parameters (although in the spring and summer months there is apparently such a relationship see page 152). It seems likely, therefore, that some chlorophyll may have been associated with the organic matter (non-oxidizable) and thus with the detritus.

The slight gradients of chlorophyll concentration recorded during the spring diatom crops in 1967 and 1968, suggest the sedimentation of the cells rather than light adaptation, since the pigment/biomass ratio did not increase with depth. ( ) However, there was a marked increase in this ratio in the Tribonema population, near the bottom of the reservoir, which may indicate some light adaption. This increase might have been due to detrital chlorophyll, but it seems unlikely as the pigment ratio 'carotenoids to chlorophylls' was lower at this depth than at any other in the reservoir (see fig 21B), which suggests that there was not an obvious detrital contamination. The variation in this ratio at the surface, middle and bottom depths of the reservoir is shown in fig 21B and the mean ratio changes compared with the mean chlorophyll concentration for the reservoir is shown in fig 21A for the period May 1967 until May 1968. The most noticeable increases in this ratio occurred soon after the decline in the spring diatom crops and also in August, apparently associated with the blue-green bloom. A much smaller increase, most noticeable near the middle of the

reservoir, occurred after the peak population was observed in the Tribonema crop in mid-September. It seems most likely that in the reservoir, this ratio indicates pigment degradation rather than 'community structure' or plankton diversity.

The increase in the particulate dry weight in the reservoir was, usually, closely associated with increases in the phytoplankton. The maximum concentrations were recorded during the spring diatom increase in 1967 (see fig 16) and in contrast with conditions in the river, the winter levels did not exceed 5.0 mg per litre and were often considerably lower than this. Similarly the organic sestonic matter in the reservoir showed a close association with changes in the phytoplankton. The correlation between the oxidizable carbon and the chlorophyll concentration in the reservoir, however, was more complex and therefore the data has been grouped to show their relationship in the summer, spring and winter periods (see fig 17). During the spring and summer periods, the correlation between these two parameters was highly significant and suggested a linear relationship. In the winter period, however, the data suggested that there was not a simple linear relationship, but that the correlation was less significant (probability 0.05). The most simple explanation is that, during the winter period much of the chlorophyll is detrital, while in the spring and summer periods, this detrital chlorophyll is overshadowed by the phytoplankton chlorophyll.

If it is assumed that the detrital chlorophyll during these periods represents only a negligible proportion of the total, the mean quantity of detrital carbon (carbon not associated with the chlorophyll) can be determined, from the regression. Thus, the detrital carbon in the spring period (March to May 1968) was approximately  $200 \text{ mg/m}^3$  whilst in the 'summer' (April to October 1967), it had increased to  $630 \text{ mg/m}^3$ . These levels are higher than those reported in the particulate seston in the North Sea (see Steele and Baird 1961), but the pattern of detrital carbon 'build-up' is apparently similar in both situations, in spite of the continual influx of river water into the reservoir. This suggests, perhaps, that during the spring and summer periods, much of the particulate river seston may sediment out to the bottom of the reservoir on entry into the basin, in spite of the turbulent conditions.



Although it is possible to estimate the mean seasonal variation in the detrital carbon and thus, detritus itself, this method and data cannot be used to determine this detritus more frequently. However, it seems likely that this data, in conjunction with total particulate volume measurements may give a realistic estimate of the variation on detritus in the reservoir (see page 164).

Fig. 19. The relationship between particulate carbon and chlorophyll 'a', in the Queen Elizabeth II reservoir (•) and the River Thames (+). The data has been grouped into seasons.

FIG. 19 [CONTD.]

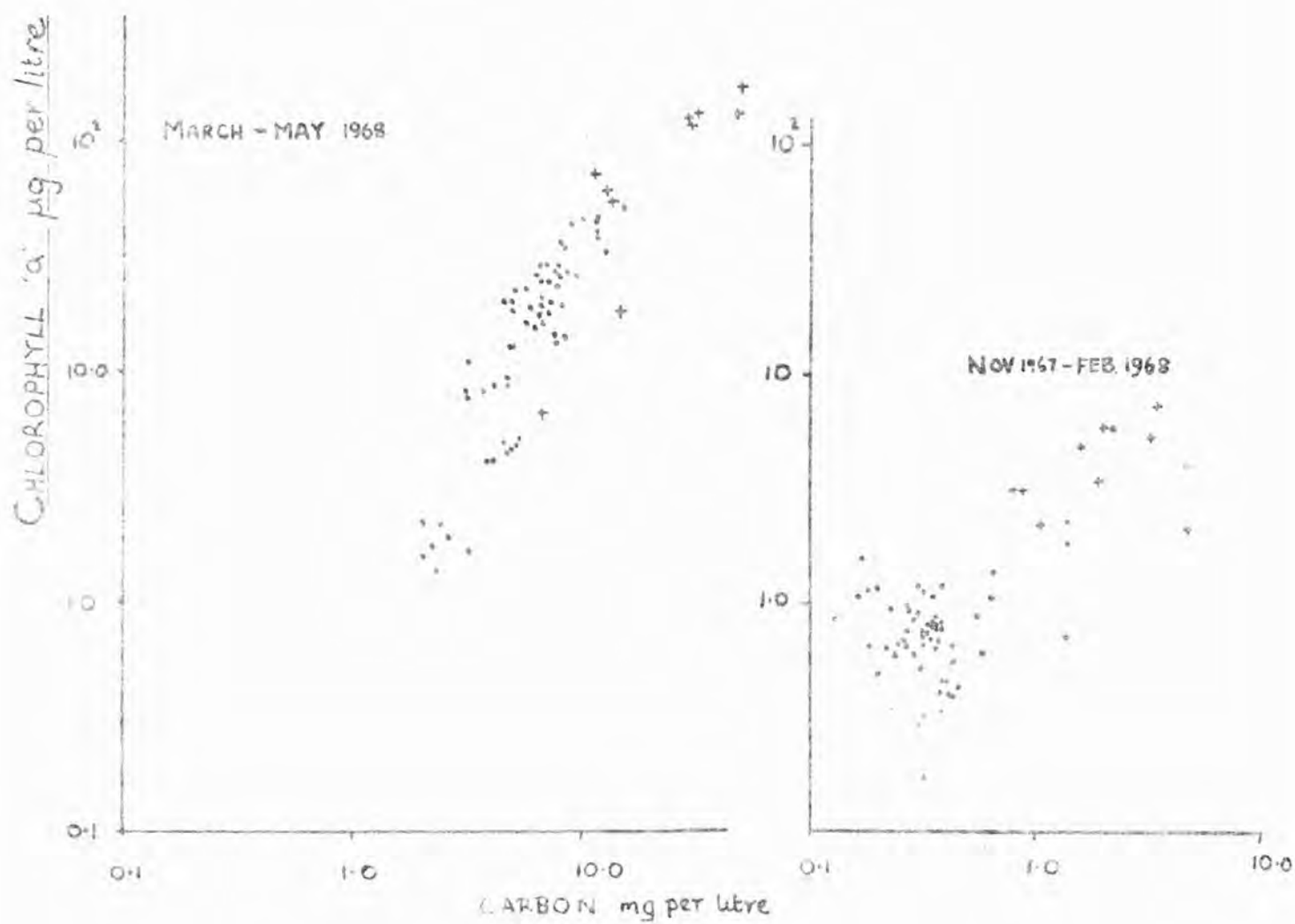


FIG. 19

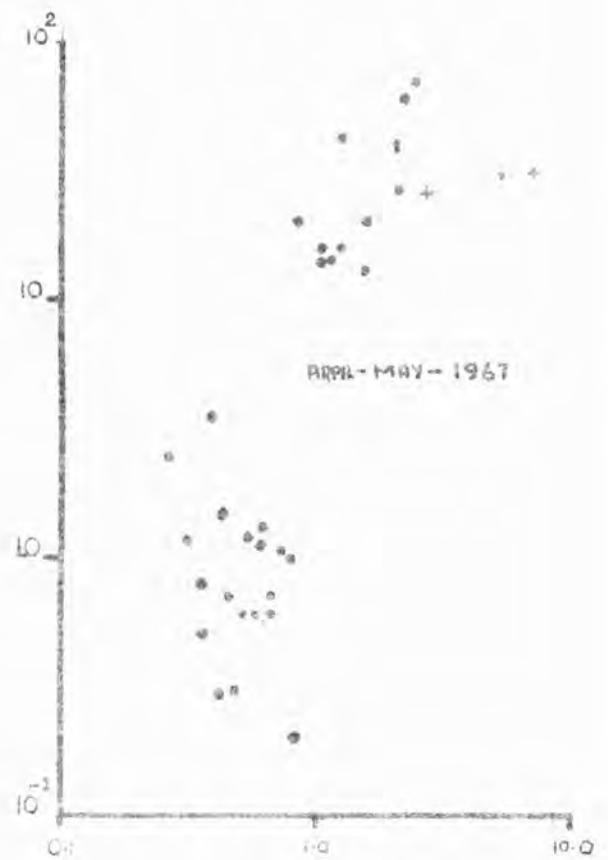
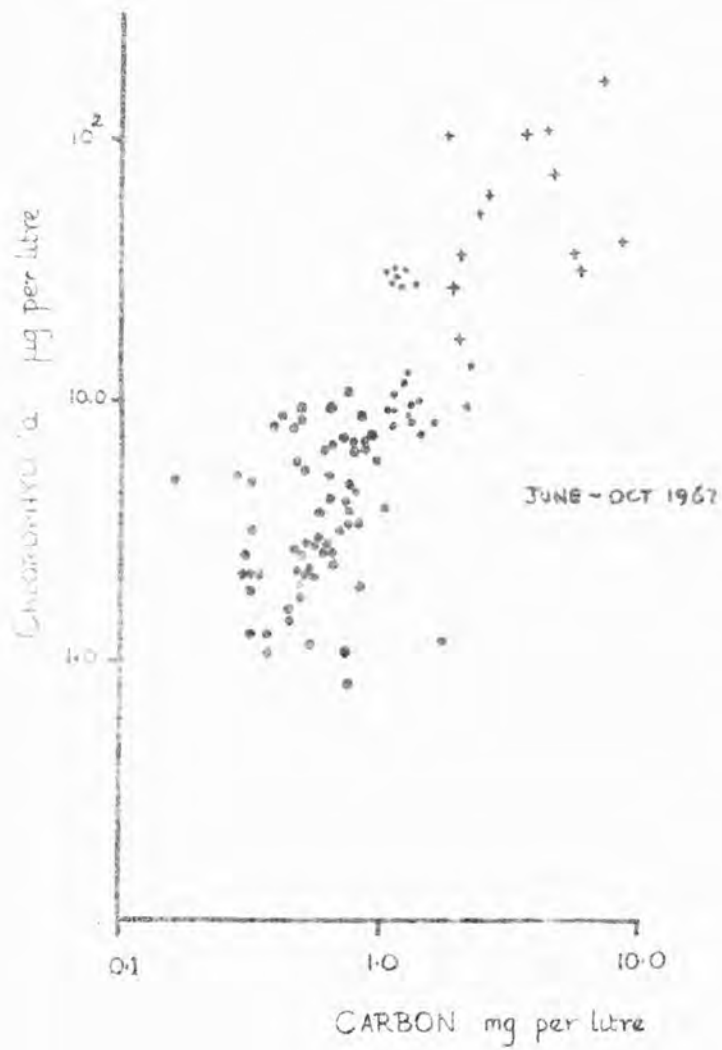


Fig. 20. The seasonal variation in the chlorophyll 'a' concentration, at the surface, middle and bottom of the Queen Elizabeth II reservoir during 1967 and 1968. Concentration of chlorophyll 'a' at 1 metre depth is indicated during periods when there was some heterogeneity in water column.

FIG. 20

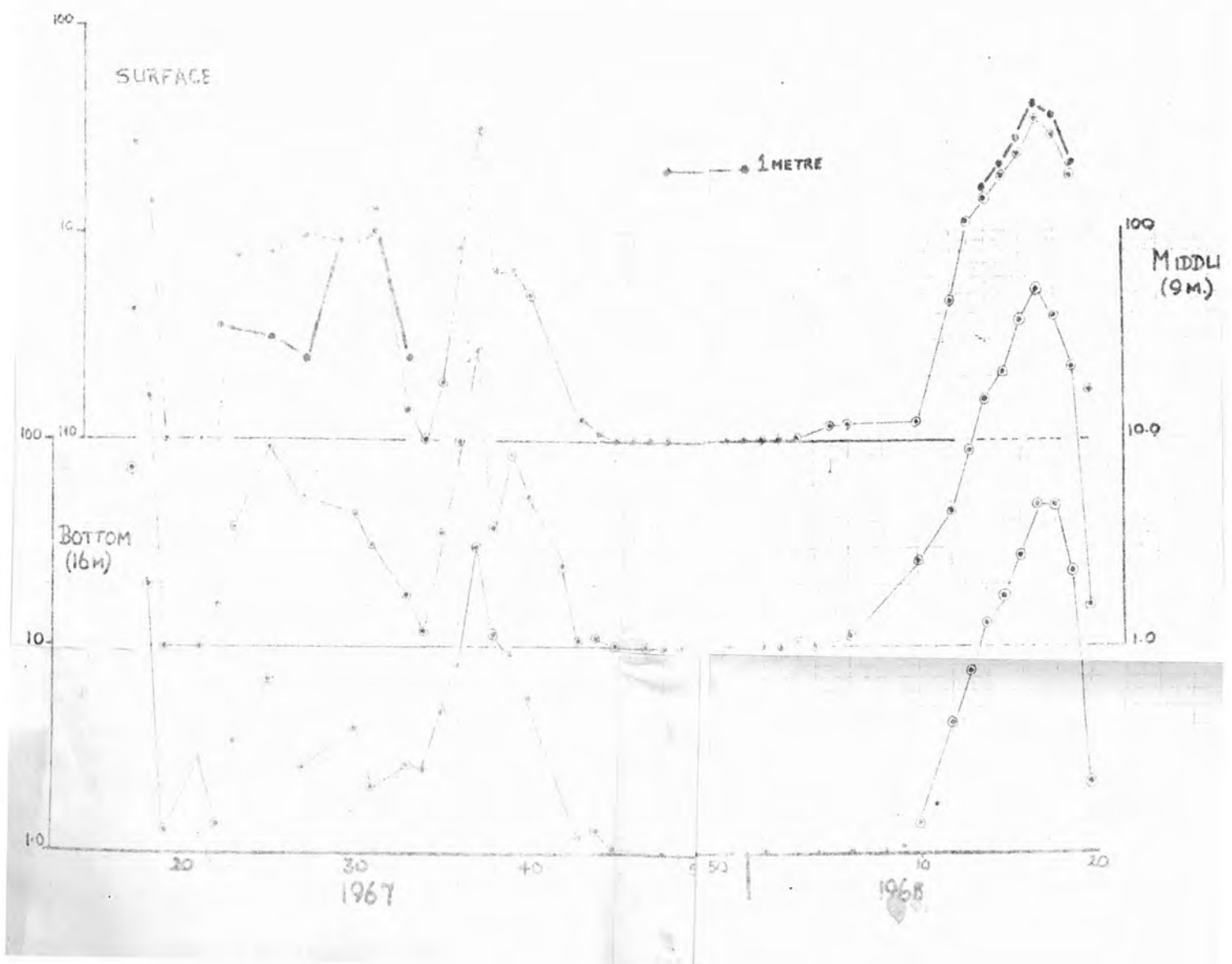




Fig. 21 (a).

Seasonal changes of the ratio between optical densities, measured at wavelenths 450 and 665  $\mu$  in methanol extracts of phytoplankton pigments, compared with the seasonal changes in the chlorophyll 'a' concentration of the standing crop in the Queen Elizabeth II reservoir and the River Thames inflow.

FIG. 21A

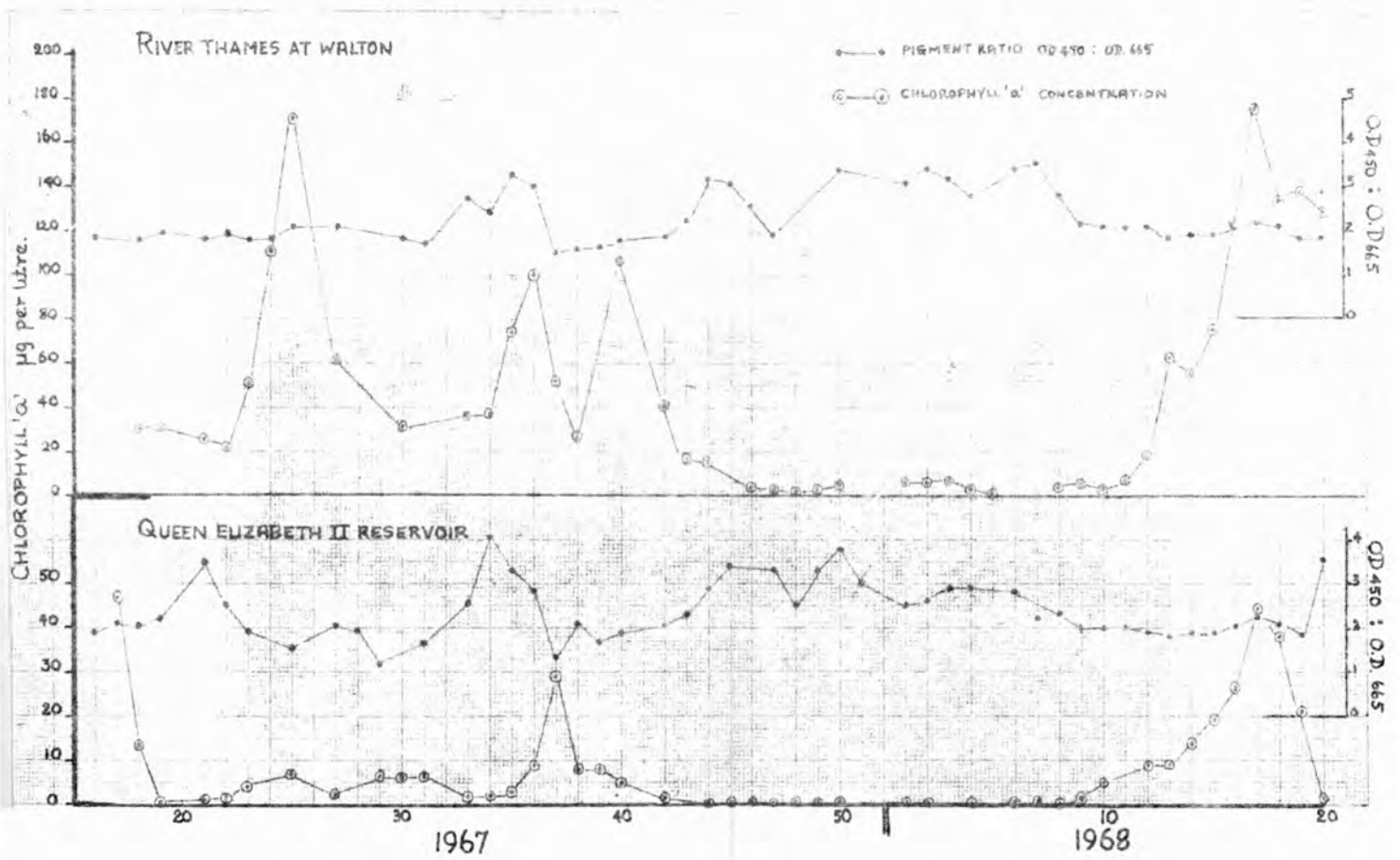
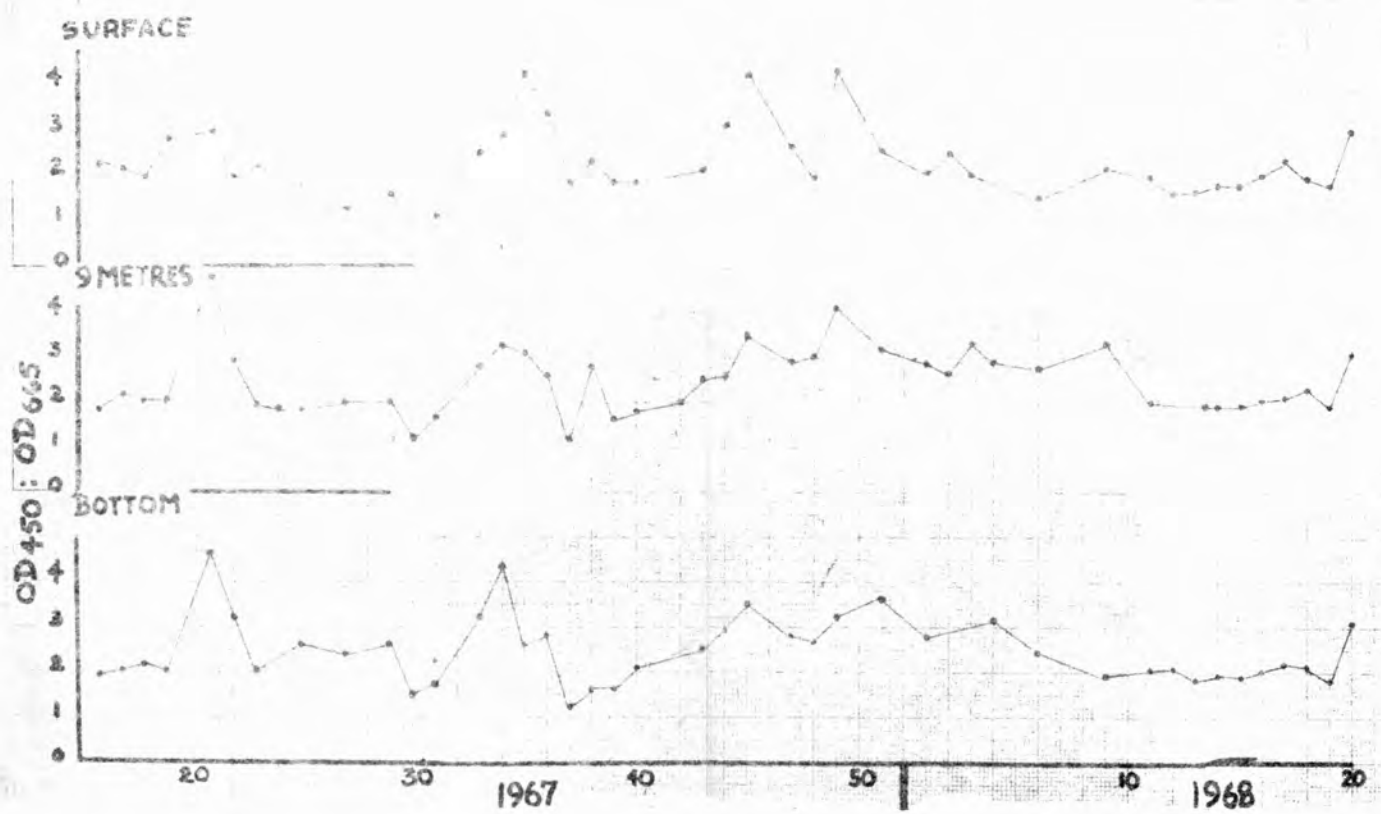


Fig. 21 (b). The seasonal variation in the ratio between the optical densities measured at wavelengths 450 and 665 mμ in methanol extracts of phytoplankton pigments, at the surface, middle and bottom of the Queen Elizabeth II reservoir.

FIG. 21B



IV. B.

4. A discussion of the seasonal variation in the phytoplankton in the reservoir and the factors which influence it.

Lund (1965) in his review on the ecology of the freshwater phytoplankton states that 'this review may be summarised by saying that much has been discovered, but that little is known for certain, about the detailed reasons for the qualitative and quantitative changes which can be observed in the phytoplankton. The number of environmental variables discovered to be of importance to planktonic organisms increases steadily, at the same time the possible effects of those known previously to be of importance enlarge,'.

Perhaps the difficulty in interpreting the environmental control of phytoplankton variation has been increased, somewhat, by attempting to consider both aspects - qualitative and quantitative - simultaneously. For although these aspects are necessarily interdependent, the environment may effect its control on both, differently. If it is considered that the succession of phytoplankton species is the outcome of interspecific competition, the environmental control of plankton quality is rather indirect, operating through its effect on the individual species and their natural selection. Thus, this aspect can only be fully understood, when sufficient information

has been gathered about the behaviour and growth of the individual species under different environmental conditions. While the directive for such information will come from the observations in the natural habitat, the source of this data, for the most part, must come from the controlled 'laboratory' experiment.

However, there is much evidence to suggest, from primary productivity studies, that the quantitative aspect of phytoplankton variation - crop production - is more directly influenced and controlled by the environment and that as Lund (1964) implies, there may be 'an upper limit to production no matter what algae predominate'. ~~( )~~

This is, perhaps, why the attempts to explain the environmental control of crop production appear to be more successful than those that attempt to explain the control of phytoplankton succession, in general, in terms of one or more factors such as illumination, temperature, turbulence or nutrients. For the same reason, it is possibly still too early in the study of phytoplankton ecology to expect that collation of data, by extensive use of the computer, from standing crop measurements, productivity studies and observations on plankton successions will help greatly, at present, in assessing the relative importance of known environmental variables in controlling both aspects of phytoplankton variation.



The following account is a consideration of some environmental variables which appear to have influenced the seasonal changes observed in the reservoir phytoplankton. The discussion on the seasonal changes of the plankton quality has been limited to factors which have appeared to influence these changes through their effect on the dominant species. For, although succession is the outcome of competition, and the patterns of periodicity indicate the ability of the species to compete against each other, the effect of the factor will depend on which species are competing and as Hutchinson (1967) suggests 'what seems to be the direct exclusion of a species by some unfavorable physicochemical factor may often turn out to be the result of the operation of this factor in determining the direction of competition; if the biological association is altered, the physical factor will appear to operate very differently'.

Although there is very little quantitative information about the phytoplankton crops in the years prior to 1966 and since the filling of this reservoir in 1962, it has been possible to determine, both from published reports (see Taylor 1963-64, 1965-66) and formalin preserved samples (taken from net hauls and routine friedinger samples), qualitative and general seasonal, changes in the phytoplankton during the earlier years. Apart from the period in which the reservoir was being filled when the plankton was reported as 'typically fluviatile', the establishment of a largely

'lacustrine' plankton was apparently rapid. Eudorina and Pandorina were recorded in July 1962 and later in August and September, Anabaena, Fragilaria, Tribonema and Volvox occurred. These genera and others - Stephanodiscus and Asterionella - were recorded regularly in the phytoplankton from 1963 and have been reported to reach 'bloom' though not 'troublesome' concentrations. The occurrence of these genera in the Thames phytoplankton and their rapid development in the reservoir can leave no doubt that the river was and still is the primary source of the plankton inoculum. However, it seems very likely that the subsequent growths of organisms in the reservoir supplement this inoculum and perhaps also, ensure the continued appearance of these genera in the phytoplankton and the formation of stable plankton associations.

The general pattern of succession, with diatoms in the spring and autumn, and the Chlorophyceae, Xanthophyceae (Tribonema) and Cyanophyceae in the summer months was apparent from 1963, but it is clear from the published reports that the standing crops (particularly the vernal diatom crops) were always small compared with those in the older Thames Valley storage reservoirs. There is some evidence that the 'age' of a reservoir may well account for, at least in part, the size of the standing crop of phytoplankton. Rozmajzlova-Rehackova (1966) reported the gradual increase in the plankton standing crop in the water-supply reservoir on the River Klicava since its filling in 1952, although the species composition

of the plankton remained virtually unchanged. The relative importance of some species did change, however, as the age of the reservoir increased and similar changes have been reported in other new reservoirs (see Sterbova 1956, Round 1956 and to a lesser extent Hammerton 1959). Sramek-Husek (1955, see ref. Rozmajzlova-Rehackova 1966) considered that 'the entire development of a reservoir up to a full balance of the biological conditions lasts about 5 to 8 years' and it is 'characterised during the first years by quantitative aberrations in some components of the plankton'. Thus it seems likely that the period of this investigation spans the later, perhaps final, stages in the stabilisation of the biology of the Q.E.II reservoir. Certainly some members of the phytoplankton such as Eudorina, Pandorina and Volvox which appeared to be common or even dominant during the early years, have been recorded only in very low concentrations (a few colonies/ml) in 1967 and 1968. Also there was a marked increase in the size of the vernal diatom crop in 1967 and 1968 compared with that in 1966, but in neither year did the crop size compare with those in other reservoirs (see Bellinger 1968, Steel personal communication). Although this increase may well be partly due to this stabilisation in the reservoir, it seems likely that other factors including physical factors and perhaps reservoir morphometry, may also be important in this respect (see page<sup>53</sup>).

Chapter V

The uses of the Coulter Counter in studies of freshwater  
phytoplankton ecology.

- (a) Findenegg (1965) states 'We shall, however, never fully understand what is going on in the primary production of a lake until we know what species occur, where and when they appear, and how they interfere with the present planktic community. We also shall never be able to estimate the share of phytoplankton in secondary production if we do not know the nutritional importance of its components.'

Whilst it is generally accepted that visual identification and direct counting are the best means, available at present, in determining the changes in the phytoplankton community, some difficulty arises in relating such data to the changes in other environmental parameters, through lack of suitable conversion factors (see for example Strickland 1960, Lund 1964). Furthermore, the inherent variability of many of the possible 'standard units' of biomass has increased this difficulty. (Westlake 1965). Perhaps the primary use of the Coulter Counter in phytoplankton ecology, is that it offers a reliable, unbiased means of quickly estimating cell volume (see for example El Sayed and Lee 1963) in cultures. This volume does not necessarily correspond exactly to the visual estimate of volume since the former represents the total volume of non-

conducting material in or around the cell (see Evans and McGill 1967) by virtue of the mechanism of the counter. However, the 'coulter volume' may be considered to give a standard reproducible estimate of volume for most species of algae. Although the validity of volume as the standard unit of biomass is questionable (see Paasche 1960, Westlake 1965), it is perhaps, the most practical and with the use of the Coulter Counter, the most precise measure of biomass at the present time.

The relationship between cell volume and cell carbon and other possible parameters of cell biomass has been investigated in several species of marine phytoplankton, with and without the use of the Coulter Counter (see for example Parsons et al 1961, Mullin Sloan and Eppley 1966 and Strathmann 1967), but there is apparently much less published work on comparable data for freshwater phytoplankton (see Lund 1964, Jorgenson 1964 and Nalewajko 1966). The results in table 7 were derived from measurements on unialgal but not axenic cultures of algae, grown under a variety of environmental conditions. The data was collected to determine the approximate relationship between cell volume, chlorophyll a content, cell carbon and dry weight in some freshwater phytoplankton in order to estimate the quantity of detrital seston in the Q.E.II reservoir (see page 164). These relationships are shown in fig 22 and the following regression equations were determined to describe algal volume (coulter volume) as a function of other parameters.



Table 7

The carbon and chlorophyll a content of some algae  
grown in culture. The data is expressed as microgrammes  
per mm<sup>3</sup>, 'coulter' volume

<u>Species</u>	<u>No. of samples</u>	<u>Chlorophyll μg/mm<sup>3</sup></u>	<u>Carbon μg/mm<sup>3</sup></u>
Tribonema ? vulgare	(5)	12.65-18.6	625-2160
Tribonema sp.	(3)	25.3-31.8	1.79-9.15
Eudorina elegans	(2)	5.86, 11.45	380, 386
Cosmarium botrytis	(6)	1.56-9.3	139-232
Euglena gracilis	(1)	1.9	
Chlamydomonas gleocystiforme	(5)	5.6-19.8	680-760
Chlamydomonas sp.	(1)	10.2	1420
Scenedesmus spp.	(1)	23.6	326
Asterionella formosa	(2)	8.0, 10.0	172, 302
Stephanodiscus astraea (net haul)	(1)	3.86	86.5
Navicula sp.	(3)	16.9-34.4	850
Melosira varians	(1)	15.5	595
Fragilaria crotonensis	(1)	22.4	448
Anabaena inequalis	(1)	54.7	1370



1. As a function of chlorophyll content.

$$V = 55.3 (C) + 52.6$$

where V is algal volume in  $10^6 \mu m^3$  and C is chlorophyll 'a' in microgrammes (df = 36 r = 0.450).

2. As a function of the total algal dry weight

$$V = 0.468 (D) + 51.004$$

where V is algal volume in  $10^6 \mu m^3$  and D is dry weight of algae in milligrammes (Df = 26 r = 0.552).

3. As a function of the 'oxidizable' carbon content

$$V = 1.489 (Ca) + 32.35$$

where V is algal volume in  $10^6 \mu m^3$  and Ca is algal carbon in microgrammes (df = 29 r = 0.657).

The three regressions were significant at  $P = 0.01$  and indicate a linear relationship between the total cell volume and these other parameters. This linearity is, perhaps, somewhat misleading since the culture conditions though varied, did not include the stage of nutrient depletion. Less predictable relationships may result when this condition is introduced (see Mullin, Sloan and Eppley 1966, Strathmann 1967) or when these parameters are considered throughout the growth cycle of individual species of algae (see for example Steele and Baird 1962).

. . . . .

Fig. 22. The relationship between algal volume (expressed as Total Particulate Volume) and (1) chlorophyll 'a', (2) algal dry weight, and (3) carbon.

FIG. 22 (1)

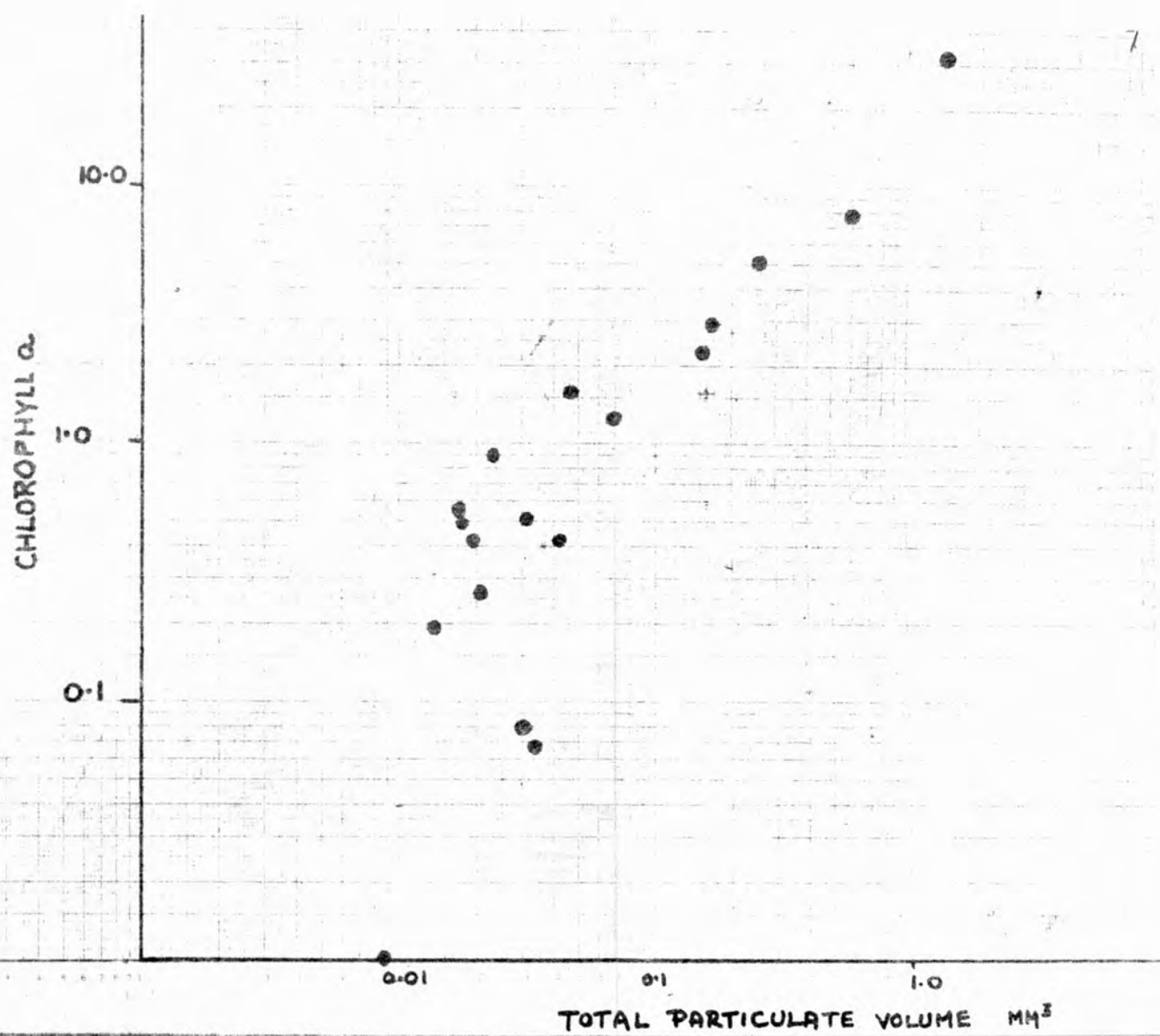


FIG. 22 (2)

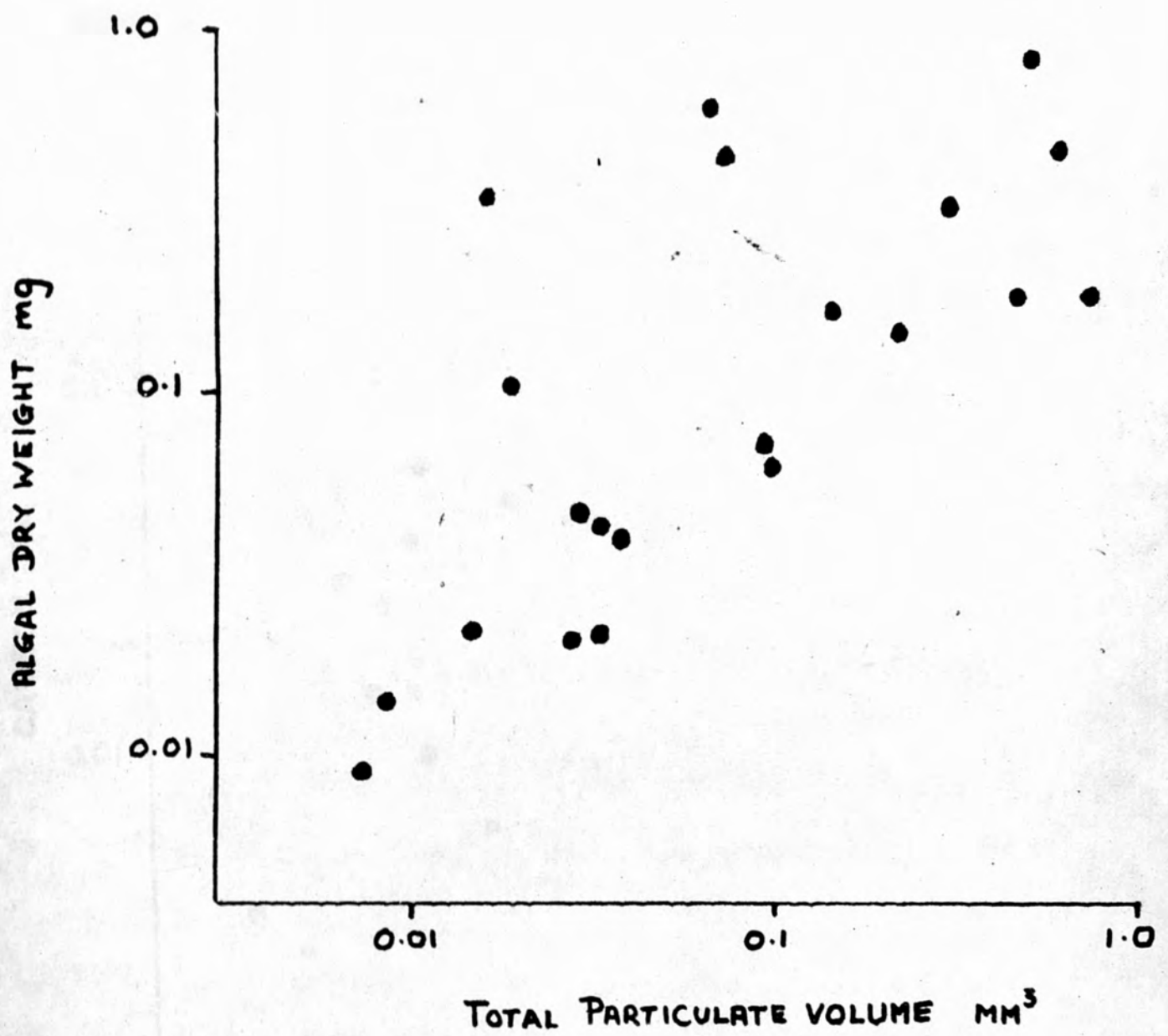
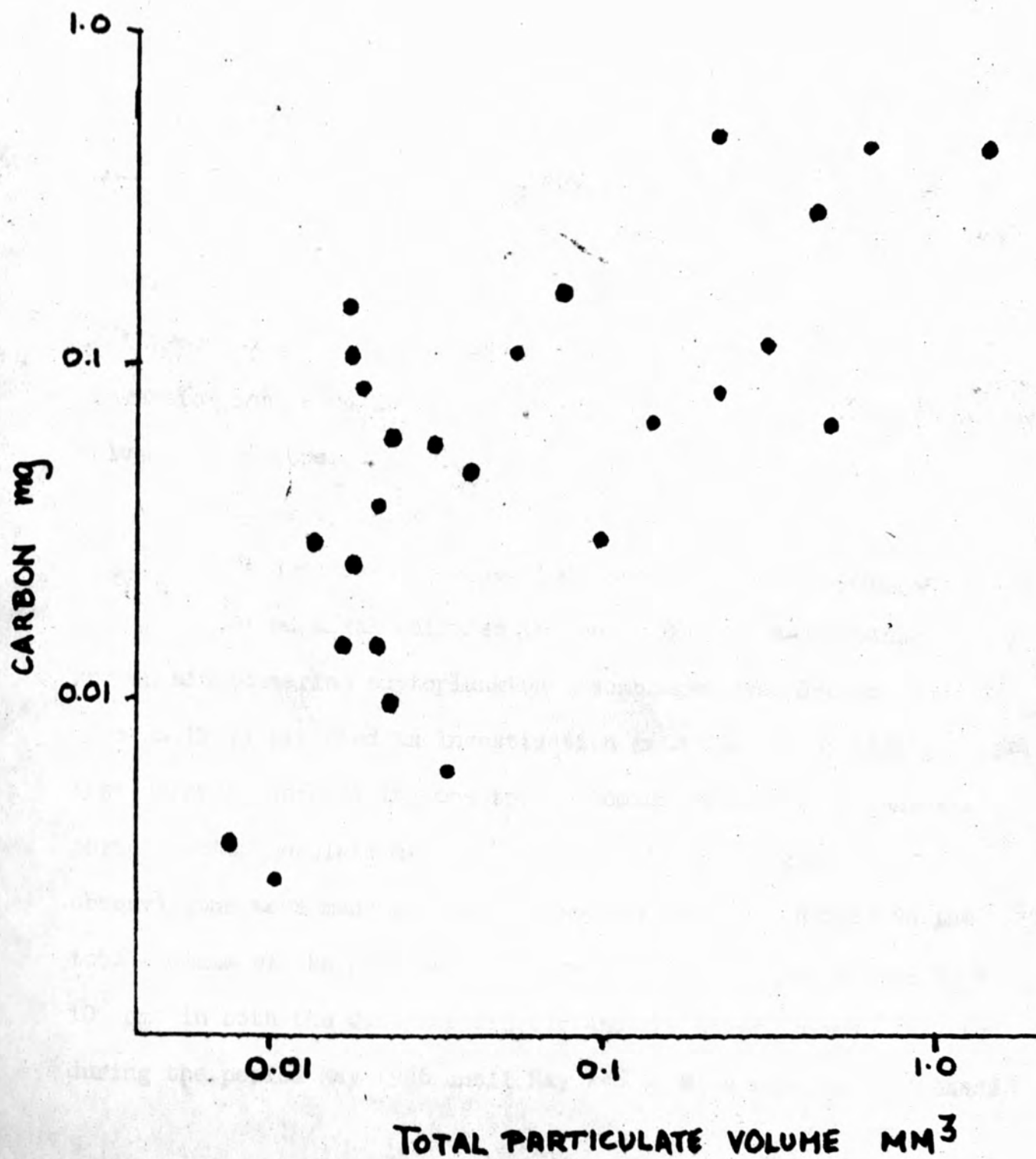


FIG. 22 (3)



(b)

The laborious nature of direct visual counting to determine the changes in phytoplankton communities has prompted the development of numerous chemical and physico-chemical methods to give more rapid, but less precise, determinations of these changes in the community as a whole (for critical reviews of these methods see Lund and Talling 1957, Vinberg 1960, Strickland 1960). The major problem in most of these methods is their inability to distinguish between detrital and living material, although the judicious combination of two or more techniques may enable some estimation of the quantity of detritus (see for example Steele and Baird 1961). Further error may be introduced into the data since much of the raw data requires conversion into some unit of biomass, the factors of which are themselves often imprecise, before the total phytoplankton biomass or standing crop is calculated.

The success of the Coulter Counter in determining the total biomass of mixed algal cultures (Maloney, Donovan and Robinson 1962) and in simple marine phytoplankton assemblages (see Sheldon and Parsons 1967) prompted an investigation into the use of this instrument in determining the total biomass of natural freshwater phytoplankton populations. As part of this investigation, observations were made on the seasonal and spatial changes in the total volume of the particulate matter in the size range  $50 - 50 \times 10^3 \mu\text{m}^3$  in both the Q.E.II reservoir and the River Thames at Walton, during the period May 1966 until May 1968. Some results from these



observations have been considered broadly in conjunction with data collected by Dr. J.H. Evans on the phytoplankton populations in other bodies of water, in the discussion on the suitability of the Coulter Counter in biomass determinations (see Evans and McGill 1968, Evans and McGill in press). Our conclusions were similar to those decided by Mulligan and Kingsbury (1968) in their independent assessment of this instrument, that 'The Coulter Counter ... provides a large increase in capability over methods previously available. It is particularly effective when used in conjunction with standard methods.'

\* \* \* \* \*

The difficulty of distinguishing detrital and living material is inherent in most non-visual techniques. However a study of the variation in the detrital seston in both the river and reservoir, has been possible following on the investigation of the Coulter Counter as reported in Evans and McGill (in publication)<sup>and</sup> is in preparation for a subsequent report.

(c) Determination of the silica content of certain diatoms

The usual procedures of determining the silica content of the diatom frustule has been either by careful cleaning and then weighing of a known number of frustules (e.g. Swale 1964) or by determining the silica through chemical analysis after the frustules have been treated to render the silica into a soluble form (see Lund 1965). Although the latter method is probably more reliable than the former, it is also somewhat time-consuming. In both procedures the result is expressed as the weight of silica per  $10^6$  cells or as a percentage of the total dry weight. Either way a comparison of the degree of silicification between different species and also between different populations of the same species is difficult if not impossible. The Coulter counter may be used to overcome this difficulty by measuring directly the volume of the frustule, from which the weight of silica may easily be calculated, as a percentage of the total volume of the diatom cell.

This method suffers from the disadvantage that the frustules must be thoroughly cleaned before the volume can be measured and thus in weakly silicified cells, they may be severely damaged and their volume underestimated. However this method is probably more reliable than weighin<sup>g</sup><sub>g</sub>, less time-consuming than the chemical analysis and introduces into the result a further parameter of cell

'biomass'.

The silica content of Asterionella formosa was determined on two separate occasions with this method when unialgal cultures, derived from isolates from the reservoir in 1966, were used, and on one occasion the silica content of a natural population of Stephanodiscus astraea was determined but the material was taken from microstainer washings which were almost entirely composed of this species. The silica content of Melosira varians was also determined from a unialgal, but not axenic culture of this diatom.

Each sample was divided into portions - the first was used to determine the total cell volume and the second, after treatment with hot nitric and sulphuric acids to remove all organic matter, to measure the total frustule volume. Microscope counts of both the cells and frustules were made to check that there was not a serious loss of material during treatment and also to ensure that a comparison between the total cell and frustule volumes was valid.

By accepting that the specific gravity of diatom silica is 2.07 (Einsele and Grim 1938 see Lewin 1953), the results, summarized in Table 8 were obtained from the following data:

1. Cell counts, and cell volumes (visual).
2. Particle counts, cell and frustule volumes (by Coulter Counter).
3. Cell dry weight, frustule dry weight and cell ash weight (i.e. weight of silica in the cell).

Using this same data, the specific gravity of the cell and frustule silica were also derived (see Table 8b).

Table 8b.

	<u>Stephanodiscus</u> <u>astraea</u>	<u>Asterionella</u> <u>formosa</u>
Specific gravity of whole cell	1.09	1.18
Specific gravity of frustule silica	3.9	3.3

(see page 168)

	<u>Stephanodiscus</u> <u>astraea</u>	<u>Asterionella</u> <u>formosa 1.</u>	<u>Asterionella</u> <u>formosa 2.</u>	<u>Melosira</u> <u>varians</u>
Mean cell volume $\mu\text{m}^3$	$2.38 \times 10^4$	322	495	2960
Mean frustule volume $\mu\text{m}^3$	$2.71 \times 10^3$	81	106.5	642
Frustule as a % of whole cell by volume	8.8%	25.2%	25.6%	21.7%
Frustule as a % of whole cell by weight	18.7% or 37%	44%	50%	75%
Silica content of $10^6$ cells by volume	$5.61 \times 10^3 \mu\text{g}$	$167.5 \mu\text{g}$	$303 \mu\text{g}$	$1.34 \times 10^3$

Table 8      Silica content, cell volume and specific gravity of selected diatoms.

Chapter VI. Culture Experiments

1. Bioassay of natural river, reservoir and lake waters during the winter 1968-1969 and spring 1969.

Although at the present time, it is generally considered that there is insufficient information to evaluate the role of water quality - particularly in terms of growth-promoting or - inhibiting substances - in controlling the succession of phytoplankton species, bioassay experiments offer, perhaps, the best approach to this evaluation.

When the test organism is taken from the same environment in which the water quality is to be assessed, the bioassay may provide more valuable information about potential crop production and the factors which limit natural crops, than can be determined by routine chemical analyses of the so-called 'major' nutrients.

In the following bioassay experiment, an attempt has been made to investigate the possibility that water quality, in spite of the apparent abundance of nutrients, may influence the phytoplankton succession and crop production in the Q.E.II reservoir and the River Thames and for the purposes of comparison only, in a small organically-rich eutrophic lake - Virginia Water lake at Englefield Green Surrey (see Evans 1964 and Evans and McGill in press for further information on this lake chemistry).



Three test organisms, in unialgal but not axenic cultures, were used to assess the water quality, but only two of these species were isolated from the reservoir phytoplankton. These species - Asterionella formosa and Tribonema ?vulgare - were maintained easily in a defined medium in the laboratory since their isolation in 1966. The third species - Anabaena inaequalis - was included as a representative of the Cyanophyceae although its source was not known. Of the three species, this alga was also the most difficult to maintain in culture so that the results in the bioassays are rather doubtful and have been included for comparative purposes only.

Bioassay tests were carried out at mostly fortnightly intervals from October 1968 until May 1969, on freshly collected water, and each experiment lasted for 12 days. At the end of this period, the growth of the test organisms in the natural, filtered water was compared with that in a standard synthetic medium. Samples of water were collected from the River Thames at Old Windsor (although this source was some 12 miles from the inlet to the reservoir, it was considered that the quality would probably not alter significantly between these points), the waterfall outlet in Virginia Water Lake and from about 3 metres depth near the outlet pier in the Q.E.II reservoir. The specific conductivity of each sample was determined before filtration through glass fibre

pads and membrane filters under aseptic conditions. Although this procedure may not have removed all the natural bacterial or nanoplankton population and the particulate matter, it is considered that this technique is preferable to heat sterilisation. Marked contamination by bacteria was not observed, and although on two occasions, there was some growth of a small 'chlorella-like' organism, it occurred in cultures which were left longer than 12 days. The particulate residue on the glass fibre pads were used to determine the quantity of sestonic particulate matter in the water (see fig 23).

The standard synthetic medium was prepared freshly from analytical-grade chemical stock solutions at least 24 hours before each bioassay. The recipe for this medium was modified from the Rodhe 8 medium (Rodhe 1948) and was as follows:-

$\text{Ca}(\text{NO}_3)_2$	= 60 mg/litre of medium
$\text{MgSO}_4$	= 5 mg/l of medium
$\text{K}_2\text{HPO}_4$	= 5 mg/l of medium
Sodium Silicate (Waterglass)	= 16 mg/l of medium
Trace metal mixture	= 5 ml/litre

The Trace metal mixture was taken from the recipe for T.M.2 (Droop 1957) and was kept as a concentrated stock in a refrigerator.

Aliquots (50 ml) of medium were put in precleaned pyrex glass flasks with cotton wool stoppers, and steam sterilised at 15 lb/sq. in. pressure for 20 minutes. Aliquots of similar volume from the filtered natural waters were transferred to flasks which had been presterilised at the same time as the synthetic medium. Each bioassay experiment consisted of 36 flasks as each 'treatment' was carried out in triplicate, to reduce any illumination variation. The test organisms were maintained in the synthetic medium and in order to achieve some standardisation in the inocula from experiment to experiment, the inocula were always taken from 14 day old cultures. These cultures were set up and grown under the same conditions as the bioassay cultures, such that the inoculum for each experiment was taken from cultures grown in the preceding experiment. Tribonema and Anabaena filaments were broken up with ultra-sonic vibrations, without any apparent deleterious effect, before inoculation so that possible errors from a variation in the inocula between bioassay cultures were minimised. All cultures were kept in a cold cabinet at 14-15°C under a single fluorescent light of approximately 2000 lumens/sq.ft. illumination in a 12-hour cycle of alternating light and dark. The bioassay cultures were placed in a 'latin square' formation. The growth in each culture was determined optically in a Eel 'Colorimeter' with a blue filter B10, but it was the total yield - dry weight of algae - from the triplicate cultures combined which was used as the criterion in assessing the

water quality. The yield from each of the natural waters (see table 9) was estimated as a percentage of the yield from the standard 'control' cultures, and the results are shown in fig 23.

The yield in the lake water was consistently lower than that from either the river or the reservoir waters and usually lower than the yield from the 'control' medium. Although this was probably due to the marked differences in nutrient concentrations in these three waters, there was not a simple relationship between the specific conductivity and the total yield in either water. Similarly there was no apparent correlation between the particulate seston load in the natural waters and the final yield of algae in the bioassays.

From October 1968 until March 1969, the river and reservoir waters were capable of supporting large populations of Asterionella and the yields were greater in both waters than that in the control cultures. It seems, therefore, that while this synthetic medium is 'adequate' for Asterionella, it does not compare with the natural waters. The difference must lie in the natural nutrient ratios or perhaps the chelating system since this species, Asterionella formosa, is apparently autoauxotrophic (see Provasoli 1958). The reduction in yield in these waters during March, April and May seems to be associated with the decrease in silica concentration, although in the May bioassay the yield of 2.4 mg/150 ml

Table 9

The Yield of algal material (expressed as milligrammes oven-dry weight per 150 mls of culture medium) in natural waters and a synthetic medium

Bioassay Organism	Source of Water	Culture Number												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Asterionella	(1) Q.E.II Reservoir	6.2	-	8.9	6.0	3.0	8.7	5.4	3.0	5.3	3.9	6.5	3.7	2.4
	(2) River Thames	8.1	-	10.7	4.5	5.2	6.8	8.6	3.3	6.4	6.4	8.4	4.7	5.3
	(3) Virginia Water Lake	3.3	-	3.7	1.5	1.3	0.8	2.9	1.0	1.0	2.1	4.2	3.9	2.2
	(4) Modified Rodhe R.8 Medium	2.7	-	7.5	1.2	0.6	3.2	2.5	1.8	1.9	4.3	12.9	6.6	11.2
Tribonema	(1)	6.0	5.2	5.7	4.0	2.7	2.2	3.1	2.2	3.1	3.1	12.6	3.4	12.4
	(2)	10.8	12.8	5.4	3.4	2.6	-	2.5	3.0	-	6.1	23.8	5.6	18.3
	(3)	3.3	1.6	2.4	1.0	1.2	1.6	1.1	1.2	1.7	1.3	0.8	0.5	1.6
	(4)	5.4	-	0.75	0.7	1.5	1.6	1.2	2.5	1.9	2.5	4.0	2.0	2.7
Anabaena	(1)	7.8	1.8	2.9	0.4	1.0	0.9	0.5	1.6	0.7	1.6	13.9	0.9	2.1
	(2)	7.2	2.1	3.3	1.8	2.0	1.0	0.8	2.3	1.4	2.1	6.9	0.3	5.0
	(3)	1.8	4.6	0.3	1.0	0.9	0.8	0.7	1.1	1.0	0.5	2.2	0.2	0.1
	(4)	5.1	4.6	2.2	1.0	1.0	1.1	0.2	2.5	1.8	2.3	14.3	1.1	2.7
Culture Number		Duration of Bioassay Experiment												
1		From 1.10.68 to 15.10.68												
2		17.10.68 - 31.10.68												
3		<del>3.11.68 - 17.11.68</del>												
4		18.11.68 - 2.12.68												
5		4.12.68 - 18.12.68												
6		18.12.68 - 1.1.69												
7		15.1.69 - 29.1.69												
8		5.2.69 - 19.2.69												
9		19.2.69 - 5.3.69												
10		5.3.69 - 19.3.69												
11		28.3.69 - 11.4.69												
12		16.4.69 - 30.4.69												
13		16.5.69 - 30.5.69												
7		29.1.69 - 12.2.69												



of reservoir water (16 mg/l) was obtained when the initial silica content was about 1 mg/litre. The low yield in the lake water, at this time however, does not appear to have been due to silica depletion, since there was an appreciable amount of this element present at the end of the bioassay. The total yield of 2.2 mg/150 ml of lake water was far in excess of the observed natural crop in the lake during the spring increase. Similarly, the yields obtained in the filtered river and reservoir waters were in excess of the quantities of this alga observed in the natural habitat, although there was apparently a close correspondence between the bioassay yield and the total diatom crops observed during the spring of 1968 and 1967. While silica depletion may contribute to the spring diatom crop decline, it seems unlikely that this is the sole or even prime cause.

Although Tribonema appeared to grow best in the filtered river and reservoir water during most of the experiment, there was a period in January and February 1969, when the growth in these waters was similar to or less than that in the control medium. This suggests that, at this time, there was some 'factor' adversely affecting growth, or alternately, some growth-promoting 'factor' (present in the later spring and earlier winter samples) absent from the water. However, even though the exact nature of this factor is unknown, it does seem likely that water quality can influence the yield and the occurrence of organisms. Tribonema growth in the filtered lake water was poor throughout the experiment and only in



two of the bioassays did the yield exceed that in the control. Usually the cultures appeared to be moribund before the end of each bioassay, although there was some growth initially. This genus is rarely observed in the Virginia Water Lake (Evans personal communication) and it seems likely that its absence in the plankton may be closely linked with the water quality and perhaps the presence of an 'inhibitor' in the water. Johnston (1963) found evidence for a link between water quality and the occurrence of Skeletonema costatum in the sea.

The growth of Anabaena in the bioassays was erratic in both the natural waters and the control medium. Usually there was a smaller yield in all the filtered waters compared with the control, although in both the November and December assays the best yield occurred in the river water. The apparently marked yield in the filtered waters at the end of January is misleading since the control cultures failed to grow. This organism was not isolated from the reservoir or the lake and thus, while the results are negative or inconclusive with respect to the bioassay, they suggest that it is unlikely that these waters will support a large population under natural conditions.

Although the bioassay has been too short to produce any conclusive evidence about the effect of water quality on the seasonal succession of phytoplankton in these waters, the results do suggest that there may be an effect. While it is unlikely that water

quality is of major importance, in this respect, in the river or reservoir, it is possible that water quality may contribute through its effect on interspecific competition.




- Fig. 23 (a). The dry weight of particulate seston and conductivity of natural waters of the River Thames at Walton; Queen Elizabeth II reservoir and Virginia Water Lake.
- (b). Dry weight yields (expressed as a percentage of the yield in a defined medium) in natural water from the River Thames (  ), Queen Elizabeth II reservoir (  ) and Virginia Water Lake (  ).

FIG. 23 A

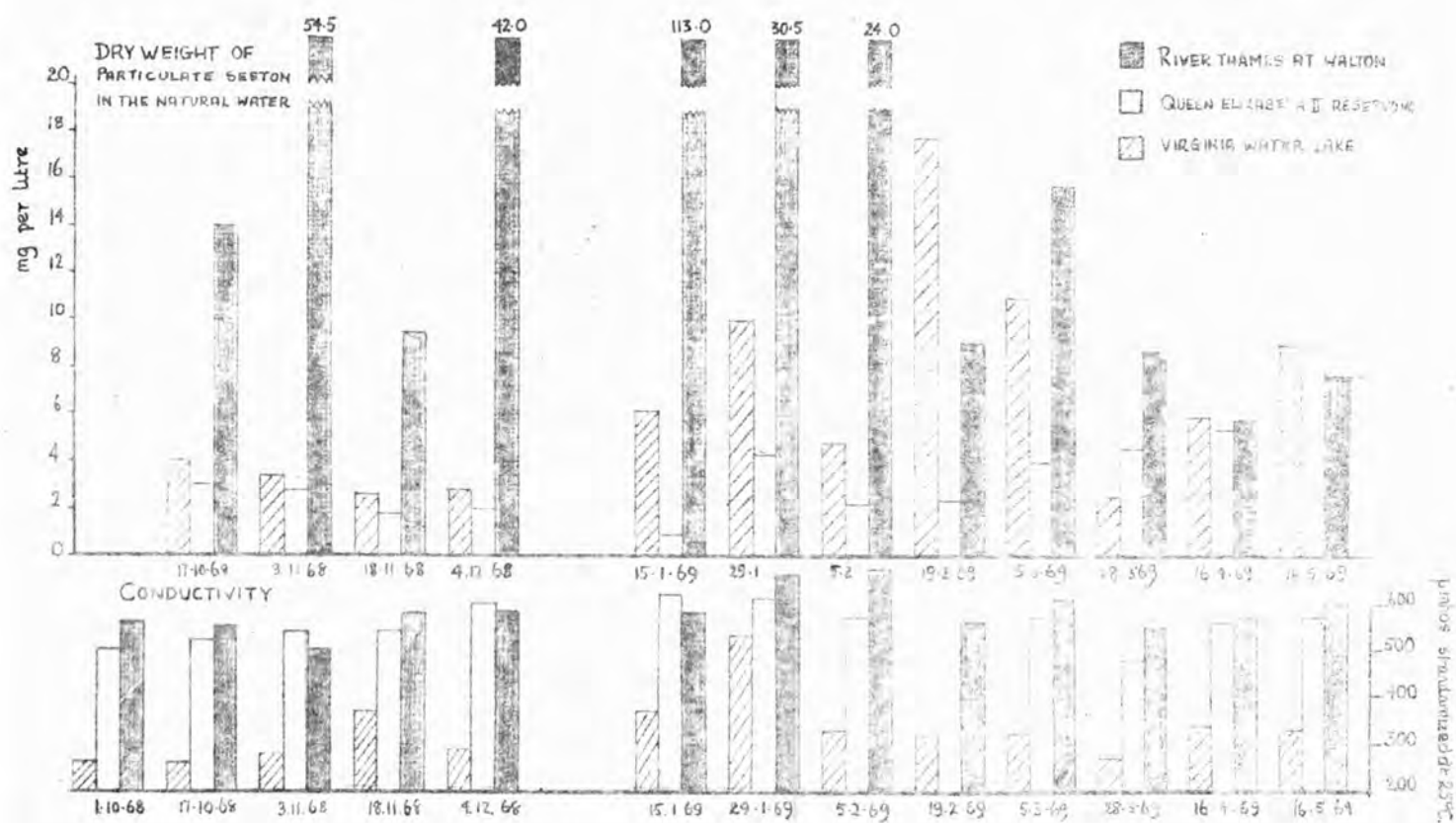
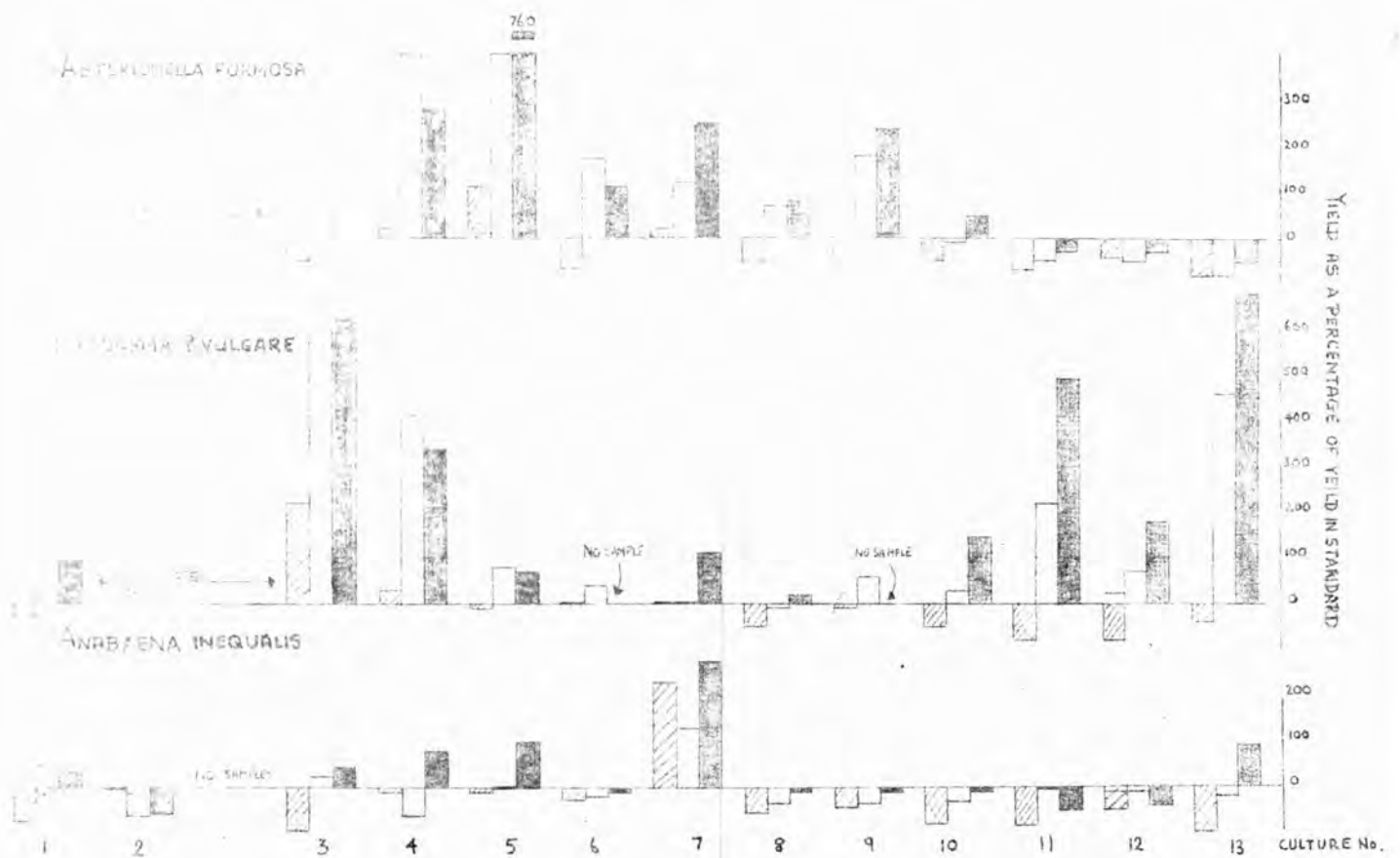


FIG. 23 B



VI

2. Potential growth rates in the natural phytoplankton population in the Q.E.II reservoir during the spring 1968.

The detailed patterns of phytoplankton periodicity and the changes in the total crop biomass can only be fully resolved, with respect to causal factors, when there is an adequate knowledge of the growth responses of the natural populations to their environment. At the present time, there is no general agreement on the best techniques to measure these responses, although there have been several reviews of the available methods (see Lund and Talling 1957, Strickland 1960).

The continual throughput of water in the Q.E.II reservoir prevents any relatively simple assessment of growth increases in the phytoplankton population, by such methods as following the rate of change of the standing crop or even, nutrient uptake with time. In the spring 1968, an attempt was made to assess the growth response of the natural population in the reservoir to the environmental factors of illumination and temperature. Although it is generally accepted that these factors may be of major importance in controlling the start of the spring increase in plankton in temperate waters, other factors, such as turbulence, may be equally or even more important. Reports of earlier phytoplankton increases in some other storage



reservoirs which, being close to the Q.E.II reservoir, would receive the same illumination (incident) and perhaps have similar water temperatures, tend to confirm this possibility. The effect of the environmental factors on the Q.E.II reservoir plankton was measured by comparing a potential growth rate for 'in situ' cultures of the natural population with cultures of the same population under laboratory conditions of light and temperature. The potential growth rate was calculated from the change in the total particulate volume (T.P.V.) - measured with the Coulter Counter - by the equation:

$$V = V_0 e^{-k't}$$

where  $V_0$  and  $V$  are respectively the initial volume and volume (T.P.V.) after time  $t = 6$  days, and  $k'$  is the potential growth rate.

In spite of the many valid criticisms, it was decided to use this method, since all attempts to obtain axenic cultures of the dominant spring diatoms and in particular, Stephanodiscus astraea, failed. It was hoped that, providing the experimental time was short so that severe contamination of the cultures by 'weeds' or bacteria did not occur, a fairly realistic assessment of the potential growth rates for these species, under enforced competition, could be made. However, the volume ranges of the small centric diatoms and Asterionella were not sufficiently distinct from each other, to allow the direct assessment of the individual growth rates. Thus, this

assessment had to be carried out by microscope counts, so that these rates were only occasionally determined (see page 184 and table 10). Nevertheless, this method does give a direct measure of the total crop response, which requires no further correction or conversion.

The potential growth rate of the natural phytoplankton population was determined at weekly intervals from mid-February until mid-May at the end of the spring diatom increase. The natural population was taken from a composite reservoir water sample which had been assembled from the aliquots from each routine bulked depth sample (see page 10). In order to keep the initial inoculum of cells fairly small, further dilution of this composite sample with filtered reservoir water, was occasionally necessary. Large zooplankton animals were removed from the sample by pipetting, but no attempt was made to remove or even estimate the small Rotifers or Ciliates. The T.P.V. in the composite sample was determined after the six sub-samples - to give three experimental cultures in duplicate - had been removed. One set of duplicate cultures, in 250 ml round-bottom pyrex flasks, were suspended from the outlet pier (see fig 1) at a depth of about 1 metre below the surface of the reservoir. The other two sets of cultures were kept in the laboratory at temperatures of 5-8°C and 14-15°C under fluorescent lighting which was maintained in a 12-hour cycle of light and dark. The illumination was approximately 1,800 and 2,200 lumen/sq.ft. respectively, but for the purposes of this experiment this difference

Table 10

Potential growth rates ( $K^1$ ) in selected algae under  
different culture conditions

Algae	Date of Culture	Reservoir "in situ"	In Laboratory	
			5 - 8° C	14 - 15° C
Small centric diatoms	6.3.68	0.014	0.135	
	13.3.68		0.458	0.430
	27.3.68	0.134		0.224
	10.4.68	0.107	0.057	0.041
	1.5.68	0.252	0.275	0.236
Stephanodiscus astraea (cell volume about 16000 $\mu\text{m}^3$ )	27.3.68	0.096	0.105	0.182
	10.4.68	0.160	0.131	0.082
	1.5.68	0.071	0.032	0.038
Asterionella formosa	6.3.68	No growth		
	27.3.68	0.156		
	10.4.68	0.242	0.275	0.160
	1.5.68	0.168	0.127	0.160
Nitzschia acicularis	10.4.68	0.281	0.292	0.297
	1.5.68	0.327	0.248	0.294

is considered to be insignificant and therefore it has been assumed that the illumination was 2000 lumens/sq.ft. and that any differences in response in the laboratory cultures are related to temperature and not light. These cultures were shaken, by hand, each day to prevent settlement and growth on the walls of the flasks, but the reservoir cultures were not moved until the end of the experiment. The change in the T.P.V. was determined after six days in all the cultures and the potential growth rate for each set of conditions was calculated from the mean T.P.V. values. The calculated growth rates ( $k$ ) are given in table 11 and a comparison of the fluctuations in these rates with the change in the natural phytoplankton population observed in the reservoir is given in fig . Although there was a small increase in the 'in situ' growth rate during mid-March, the maximum potential growth rate did not occur until mid-April when the maximum increase in the phytoplankton standing crop was also observed. During the rest of April and in early May there was a decrease in the potential growth rate, but at the end of this month it had started to increase again. The very low rate which was measured during the 17th to 23rd April was probably partly due to the growth of diatoms on the outer surface of the flasks, causing a marked reduction in the light available to the cultures. However, the overall decrease in the potential growth rates at this time was probably also a reflection of silica depletion in the reservoir. Apart from the data collected in May, the calculated growth rates in the

Table 11

Potential growth rates ( $K^1$ ) in the natural phytoplankton population of Q.E.II reservoir from February until May 1968

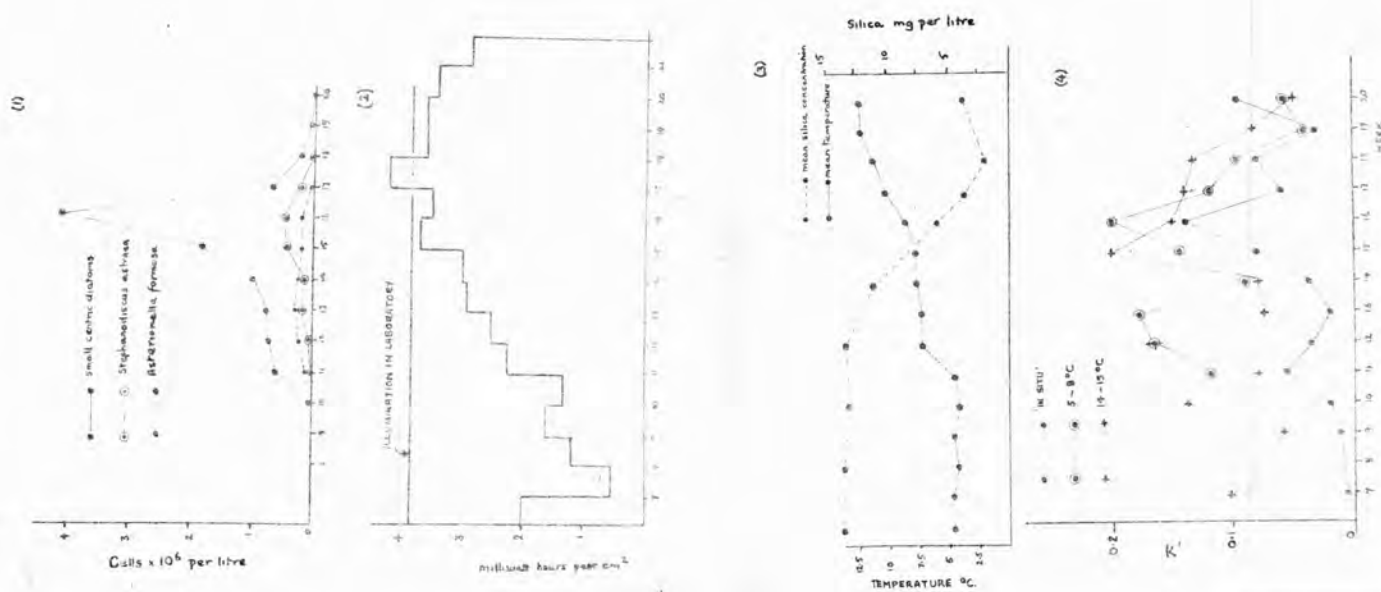
Date	Reservoir "in situ"	Laboratory	
		5 - 8° C	14 - 15° C
14.2.68	0.007		0.105
28.2.68	0.011		0.061
6.3.68	0.024		0.138
13.3.68	0.059	0.120	0.079
20.3.68	0.037	0.164	0.164
27.3.68	0.023	<b>0.173</b>	0.074
3.4.68	0.041	0.088	0.079
10.4.68	0.083	0.145	0.200
17.4.68	0.140	0.201	0.149
24.4.68	0.060	0.110	0.140
1.5.68	0.082	0.098	0.139
8.5.68	0.032	0.042	0.070
15.5.68	0.097	0.058	0.049

laboratory cultures were always greater than those for the 'in situ' cultures. This suggests that there is some light limitation of growth even at 1 metre in the reservoir throughout the earlier spring period, although it becomes less as the total daily incident radiation increases. This was confirmed by a positive correlation between the weekly mean radiation and the potential 'in situ' growth rate (see fig 24) when there was no silica limitation. The effect of temperature on the natural population and the potential growth rates are difficult to interpret. The potential growth rates of the cultures at 5°C were generally greater than those for the 15°C cultures in the experiments carried out during March while the reverse was true for the period April to May. The high value for the growth rate of the 5°C culture for the week 17th to 23rd April, is somewhat misleading since there was a marked difference in the T.P.V.'s of the duplicate cultures. There seems to be two possible explanations for these results. If it is assumed that the phytoplankton population is composed entirely of species with defined thermal requirements, or perhaps and more likely, with distinct thermal ecotypes, the difference in response of the population to the culture conditions would reflect the nature of the ecotypes present initially in the natural population in the reservoir. Thus during March the predominant ecotypes in the reservoir would have thermal optima near or at 5°C whereas in April and May these would be gradually replaced by ecotypes with optima near to 15°C or perhaps



Fig. 24 (1) The mean concentration of the co-dominant diatoms in the Queen Elizabeth II reservoir in the Spring 1968; (2) The weekly mean radiation levels incident at the surface of the reservoir compared with the culture illumination; (3) The mean temperature and silica concentration in the reservoir; (4) Potential growth rates ( $K'$ ) in the reservoir and laboratory cultures.

Figure 24



higher. Such an explanation could account for the increase in the 'in situ' growth rate during the week 13th - 19th March. The experimental cultures were dominated by very small centric diatoms with cell volumes about  $100-200 \mu\text{m}^3$ . A population of small centric diatoms with a similar volume range were observed to reach maximum concentration in the River Thames phytoplankton on the 20th March and it seems very likely that these diatoms were derived from the same initial population. The river population had disappeared by the end of March (see page 104) and similarly, these centric diatoms were not seen in later cultures, except in low concentrations.

The other explanation is that, the difference in response is due to the lag period required for the cells to adapt to a higher (or lower) thermal regime. Thus, while the reservoir temperature remains close to  $5^{\circ}\text{C}$  there is a lag period in the  $15^{\circ}\text{C}$  culture so that the mean growth rate for the experiment (since the method measures the mean growth rate over the period of the experiment) is necessarily lower than the real rate. The reverse occurs when the reservoir temperature approaches more closely to  $14-15^{\circ}\text{C}$ . Lund (1919) demonstrated this ability for adaptation<sup>at</sup> in Asterionella formosa and there have been several reports of light adaptation<sup>at</sup> in algae (see Steeman Neilson et al 1962). At present, there is insufficient information to discount the possibility of thermal ecotypes or the occurrence of different, but morphologically similar, races in algal species. Certainly, such races and ecotypes occur in 'higher plants', but presumably the difficulty arises in the relatively short

generation time in algae which allows both the development of large asexual clones, and rapid ecological selection and which prevents the phytoplankton ecologist from determining such races. Adapt<sup>at</sup>ion could be the result of this rapid selection and thus the explanations could be compatible.

The reduction in the potential growths rates in all the cultures in experiments carried out at the end of April and early May was probably due to silica depletion. However, it seems likely that both light and temperature are the major factors influencing the phytoplankton population increase in the spring, although temperature may well affect the pattern of species succession in the population. Nutrient limitation may be very important in terminating the spring growth, even though there may be continual renewal of nutrients from the inflowing river water. Calculated growth rates in some phytoplankters in these experimental cultures are given in table 10 . These rates are not comparable to the potential rates for the whole natural population, since cell numbers and not cell volumes were used in the calculations. These rates are comparable however, with Fogg's relative growth constant  $k'$  (see table 2 page 20, Fogg 1965), although they must be considered to indicate the behaviour of the algae under stress of competition in non-standard conditions. Ideally, potential growth rates for each species of algae, or more realistically, for each of the major phytoplankton species, is required under a variety of but specified, culture conditions. While such information is being gathered gradually for

several species (see for example, Lund 1964, Jitts et al 1964) many algae have not yet been kept successfully in any form of culture. Therefore the use of natural mixed populations in crude culture is necessary since this approach may be the only available method with which to assess growth behaviour. Although there is insufficient data, from the above results, to be of much real significance, there are several interesting features.

The growth rate for the small centric diatoms, which included Stephanodiscus hantzschii, in the 'in situ' reservoir cultures appears to reach a maximum after the main reservoir crop had decreased considerably. Thus, it seems possible that some other factor (or factors) and not nutrient depletion was responsible for this decrease. The maximum rate corresponds closely to the rate for Stephanodiscus hantzschii under similar conditions of light and temperature, but in unialgal culture. (Swale 1963). If this is a real and not an illusionary similarity, the reduced growth rates observed in the experiment during 10th to 16th April may have been due to competition with the other phytoplankton and not, as in the earlier experiments, to the light and temperature. The three other diatoms, for which growth rates were measured, appeared to have greater rates of increase during this week, than those calculated for the small centric diatoms, although the maximum rates in both Asterionella formosa and Nitzschia acicularis were fairly close to that observed

in the small centric diatoms. However, the growth rates for Asterionella observed during these experiments are considerably lower than that determined by Lund (1949) for the Windermere Asterionella. This is most probable due to the difference in temperature and possibly also light in the culture conditions, since a growth rate of  $0.38 \log_{10}$  units was obtained in a unialgal culture of the reservoir Asterionella at  $5^{\circ}\text{C}$ , in a completely separate growth experiment. In both Asterionella and Stephanodiscus astraea, there was a decrease in growth rate during the experiment 1st to 7th May. It seems likely that these two diatoms were limited by the silica depletion in the reservoir, although Nitzschia acicularis, as the small centric diatoms, did not appear to be limited since its growth rate under the experimental conditions did not alter much.



VI.

3. Perennation in certain species of phytoplankton present in the Q.E.II reservoir.

In view of the apparent lack of published information on perennation in phytoplankton organisms (see Lund 1965), it was decided to include this section in the thesis. It is emphasised, however, that the following results do no more than indicate a possible mode of survival in certain species, since this aspect of plankton ecology has only been considered in a very minor way during this investigation.

The basic experiment was designed to test the capability of Coscinodiscus rothii to survive in non-illuminated, but oxygenated silt for long periods. The apparent similarity in the occurrence of this diatom in the autumn of 1966 and the seasonal cycle in Melosira italica subsp. subartica (Lund 1954, 1955) suggested that Coscinodiscus rothii, in the absence of any observed auxospore formation, might survive at the bottom of the reservoir in some 'physiological' resting stage. Samples of reservoir silt were dredged from the reservoir near Tower B (see fig 1 ) in November 1966, (during the growth of this diatom) and then in July, August and October 1967, and also in February, March and April in 1968). As each sample was collected, it was transferred to a dark, stoppered bottle and kept in a dark refrigerator at a temperature between

0°C and 5°C. Marked deoxygenation of the silt did not occur as the air was not fully excluded from the bottles, but no attempt was made to aerate the samples except when aliquots were removed for culturing. The 'age' of each silt sample, in the following discussion, refers to the period of refrigerated storage; for example, the silt collected in November 1966 was 32 months 'old' in July 1969, whereas the sample taken in July 1967 was only 24 months 'old'. A note was made of the most common plankton present in the silt samples at the time of their collection. Usually the species composition depended on the phytoplankton and thus in November 1966, there were many cells of Coscinodiscus but in July 1967, there was a large number of Stephanodiscus astraea cells also. The 'age' of the algal species in these silt samples do not necessarily correspond to the 'algae' of the samples; for example the population of Stephanodiscus astraea observed in the July 1967 silt was probably derived from the phytoplankton population recorded in the previous spring (see page 136), whereas that observed in the silt sample collected in March 1968 was more likely to have been derived from both the July 1967 silt and the spring 1968 phytoplankton populations. Thus, although the 'July' Stephanodiscus was at least, 28 months 'old', the 'March' population may only have been 16 months 'old' in July 1969. All silt samples were kept in the dark refrigerator for 1 month, before use in the experiment to ensure that newly sedimented phytoplankton cells did not invalidate the results. The

whole experiment lasted from November 1967 until July 1968, but was composed of five sub-experiments, set up on five different occasions, during this period. Each of these sub-experiments lasted from 1 to 3 months. On each occasion, an aliquot of silt from each available sample was cultured in glass-distilled water under fluorescent lighting and at about 15°C. The presence and development of viable population was determined by the examination prior to, and within 1 to 4 weeks after, the culture had been started. The presence of viable cells - usually reproducing - in the silt in this latter examination only was considered to be the criterion for the ability of that species to survive or perennate at the bottom of the reservoir.

Although it had been planned, originally, to consider the 'fate' of Coscinodiscus rothii only, numerous other algal species developed in culture, and therefore the occurrence of the most common species was also recorded. It is from these records that the following tentative suggestions on their perennation have been based. The results are shown in Table 12 ~~Table 12~~. For each species of algae, the upper column indicates the 'oldest' silt sample in which it developed, while the lower column indicates the species presence in the other silt samples in the sub-experiment.

The effect of refrigerated storage on the development of the diatoms - Coscinodiscus rothii, Stephanodiscus astraes (cell diameter 40-50µ), S. astraes (cell diameter 20-25 µ) and the small centric diatoms (including S. hantzschii) - in each of the

Table 12

Species		Date of culture					
		Nov. 67	Mar. 68	July 68	Nov. 68	July 69	
<i>Coscinodiscus rothii</i>	(1)	12 months	16 months	No record	No record	24 months	
	(2)	4 (4)	5 (5)	0 (4)	0 (8)	1 (7)	
<i>Stephanodiscus</i>							
<i>astraea</i> (large cell)	(1)	4 months	8 months	12 months	9 months	17 months	
	(2)	3 (4)	5 (6)	3 (4)	1 (8)	1 (7)	
<i>Stephanodiscus</i>							
<i>astraea</i> (small cells)	(1)	12 months	9 months	12 months	13 months	24 months	
	(2)	4 (4)	4 (5)	3 (4)	5 (8)	6 (7)	
Other small centric diatoms	(1)	12 months	8 months	12 months	13 months	24 months	
	(2)	4 (4)	4 (5)	3 (4)	5 (8)	6 (7)	
<i>Nitzschia acicularis</i>	(1)			12 months	8 months	19 months	
	(2)			3 (4)	2 (8)	3 (7)	
<i>Nitzschia palea</i>	(1)			24 months	8 months	21 months	
	(2)			4 (4)	2 (8)	2 (7)	
<i>Surirella</i> spp.	(1)	No record	No record	24 months	8 months	24 months	
	(2)	0 (4)	0 (5)	1 (4)	2 (8)	1 (7)	
<i>Amphora ovalis</i>	(1)	12 months	No record	No record	No record	23 months	
	(2)	4 (4)	0 (5)	0 (4)	0 (8)	1 (7)	
<i>Gyrosigma</i> sp.	(1)	No record	No record	5 months	No record	No record	
	(2)	0 (4)	0 (5)	2 (4)	0 (8)	0 (7)	
<i>Navicula</i> sp.	(1)	4 months		12 months	No record	32 months	
	(2)	3 (4)		2 (4)	0 (8)	7 (7)	
<i>Fragilaria</i> sp.	(1)	12 months	16 months	20 months	24 months	32 months	
? pinnata	(2)		present in all cultures				
<i>Melosira varians</i>	(1)	12 months	16 months	20 months	24 months	32 months	
	(2)	present in	all cultures, Auxospore formation only				
			in Mar. 68				
<i>Melosira granulate</i>	(1)	12 months	No record	20 months	No record	23 months	
	(2)	4 (4)	0 (5)	4 (4)	0 (8)	1 (7)	
<i>Scenedesmus</i> spp.	(1)	12 months	16 months	20 months	24 months	32 months	
	(2)		present in all cultures				
<i>Anabaena</i> spp.	(1)			20 months	24 months	32 months	
	(2)	present in	all cultures older than six weeks				
<i>Pediastrum</i> spp.	(1)	No record	16 months	No record	13 months	24 months	
	(2)	0 (4)	5 (5)	0 (4)	1 (8)	6 (7)	
<i>Dictyosphaerium</i> sp.	(1)	No record	No record	No record	7 months	32 months	
	(2)	0 (4)	0 (5)	0 (4)	1 (8)	7 (7)	
<i>Coelastrum microporum</i>	(1)	3 months	No record	No record	No record	No record	
	(2)	1 (4)	0 (5)	0 (4)	0 (8)	0 (7)	
<i>Volvox globator</i>	(1)	No record	No record	20 months	No record	21 months	
	(2)	0 (4)	0 (5)	1 (4)	0 (8)	1 (7)	

silt samples is shown in table 13. Lund (1965) considered that 'freshwater plankton algae can be divided into three groups as regards perennation'. Firstly those species in which there is no known resting stage; secondly those algae in which spores are produced occasionally and lastly those species with life cycles which depend on the production of spores for the continuation. There can be little doubt that most of the Chlorophyceae species (including the desmids), Anabaena spp. and Aphanizomenon flos-aquae belong to the latter two groups and that their frequency in the silt culture depends on both the rate of spore germination and the initial size of the inoculum. Thus, the blue-green algae were only observed in the sub-experiments which were continued for six weeks, or more. This suggests a lag period in spore germination which could account for their absence in the sub-experiments of shorter duration. However, since these species were observed in all the silt cultures in each sub-experiment in which these algae were present, it seems very likely that the initial inocula of spores were large. The occurrence of Volvox globator in only two silt cultures throughout the experiment, suggests that there was only a small initial inoculum of spores present in the silt samples. It is possible that the source of these spores (since this species was recorded in cultures of silt taken in November 1966 and July 1967) was from the growth of the species recorded in the surface waters during June and July 1966 (see page 134).



Table 13. Presence of selected centric diatoms in cultures of mud  
deposits after their storage in the dark at low temperatures.

<u>Date of mud sample</u>	<u>Centric diatoms</u>	<u>Storage period in months</u>				
		12	16	20	24	32
November 1966	(1)	p	p	-	-	-
	(2)	-	-	-	-	-
	(3)	p	-	-	-	-
	(4)	p	-	-	-	-
July 1967		4	8	12	16	24
	(1)	p	-	-	-	-
	(2)	p	p	p	-	-
	(3)	p	p	p	-	p
August 1967	(4)	p	p	p	-	p
		3	7	11	15	23
	(1)	p	p	-	-	-
	(2)	p	p	p	-	-
October 1967	(3)	p	p	p	p	p
	(4)	p	p	p	p	p
		1	5	9	13	21
	(1)	p	p	-	-	-
December 1967	(2)	p	p	p	-	-
	(3)	p	p	p	p	p
	(4)	p	p	p	p	p
		3		11	19	
February 1968	(1)				9	17
	(2)				p	-
	(3)				p	-
	(4)				p	p



Table 13 (contd.)

		8	16
March 1968	(1)	-	-
	(2)	p	p
	(3)	p	p
	(4)	p	p
		7	15
April 1968	(1)	-	-
	(2)	p	p
	(3)	p	p
	(4)	p	p

(1) Coscinodiscus rothii

(2) Stephanodiscus astra~~ea~~ (large cells)

(3) Stephanodiscus astra~~ea~~ (small cells)

(4) Other small centric diatoms

p = present

Although it is most likely that the majority of the Chlorophycean species which appeared in the silt cultures developed from resting spores, it is possible that some were existing in the silt as facultative heterotrophs. Saunders (1957) in a list of such organisms includes species from the genera Scenedesmus, Coelastrum, Chlamydomonas and Chlorella. Many of these genera exist only in small quantities in the reservoir phytoplankton, and it seems more likely that their source is largely derived from the inflowing river water. It must be considered an advantage for survival if these algae can exist on the bottom of the reservoir through heterotrophy when they sediment out of the plankton before adequate spore production can occur. Facultative heterotrophy has also been reported in some diatoms, especially in the genus Navicula, and more rarely Nitzschia (Lewin 1953) but Hutchinson considers that it is unlikely to be found in the planktonic diatoms. If this is so, the presence of many diatoms in the silt cultures must be attributed either to spores or to some other resting stage. Auxospore formation has been reported in the genera Coscinodiscus, Stephanodiscus and Melosira, but during the period of this investigation, it was only observed on one occasion in Melosira varians, in culture. It was never observed in the other two genera either in nature or in culture. While this does not exclude the possibility of the formation of such spores in small quantities in the reservoir, it seems more

likely that both Stephanodiscus and Coscinodiscus can exist as 'physiological dormant' cells in much the same manner as has been reported for certain species of Melosira (see for example Lund 1954, 1955 and Nipkow 1950). In both genera, cells were observed, in which the cell contents were clustered near the cell centre or around the periphery (see figures 25 ): but all attempts to positively identify such cells as the resting stage, as Lund did for Melosira italica subsp. subartica filaments, were ~~un~~successful. (Lund 1954). However, on no occasion were obviously viable cells recorded in the silt cultures at the beginning of each sub-experiment.

The frequency with which Coscinodiscus cells were recorded in the silt cultures decreased markedly with 'ageing' of the silt samples (see table 12) so that in the July 1969 sub-experiment, only one viable cell was seen; in the culture of December 1967 silt; whereas in the sub-experiments of November 1967 and March 1968, viable cells were present in all the silt cultures. If it is assumed that the cells initially present in the silt samples at their collection were derived largely from the phytoplankton population recorded in the winter of 1966 (see page 135) then the maximum period of survival of cells in this population is apparently about 16 months or less (see table 13 ), in non-illuminated aerobic mud. The apparent discrepancy between the frequency

Fig. 25     Coscinodiscus rothii. Cells observed in cultures of mud deposits from the Queen Elizabeth II reservoir

a) and b)     ? dormant cells with distorted cell contents, in valve view

c) and d)

              c)     Similar cell in three-quarters view

              d)     Viable cell with turgid cell contents in girdle view

e) and f)     viable cells from cultures, in valve view

Figure 25 a) and b)

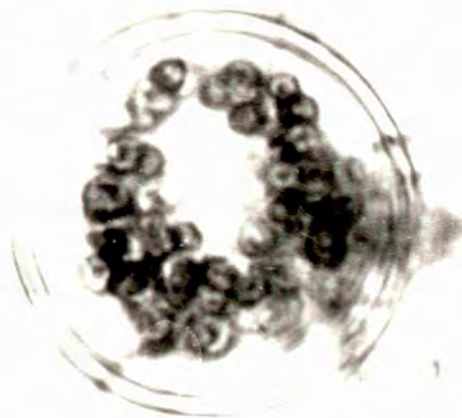
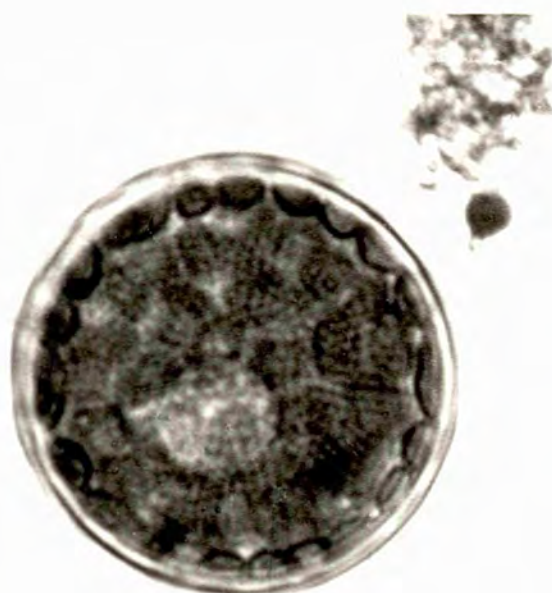


Figure 25 c) and d)





Figure 25 e) and f)



of occurrence of this species in the November 1966 silt and the silts collected at later dates is resolved when the 'age' of the cell population is considered. Thus, the cells had already been 'dormant' in the silt for 8 months when the sample was collected in July 1967. Since there was a small population of Coscinodiscus rothii recorded in the reservoir phytoplankton in the autumn 1967, it is possible that some of the cells in the silt collected in December 1967 were derived from this population and not the previous one. In such an event, the age of the inoculum from which the viable cell was derived in sub-experiment July 1969, would be 20 months and not as expected, 35 months.

It is apparent that if this species is able to survive for at least 16 to 20 months at the bottom of the reservoir, its position in the phytoplankton of the reservoir is, theoretically, assured providing there is sufficient turbulence to allow some replenishment of the inoculum. However, if the water turbulence remains low enough to prevent the resuspension of the cells, the species will gradually be excluded from the reservoir basin, unless a new source of inoculum - presumably from the river inflow - occurs. During the period of this investigation, Coscinodiscus rothii was not recorded in the river plankton and neither had this species been reported in any known published work on this river or

its tributaries (Fritsch 1902-3, Rice 1938, Swale 1964).

A similar pattern of survival is probable for larger cells of Stephanodiscus astraea (cell diameter 40-50 $\mu$ ) although the possible source of cells in the silts is less easy to trace, since this species was frequently observed in small quantities in the winter river plankton. However, if it is assumed that most of the cells were derived from the spring phytoplankton population in 1967 and 1968, the survival period appears to be approximately 16-20 months for each population.

It is not possible to determine the probable age of either the small Stephanodiscus astraea (cell diameter 20-25 $\mu$ ) or the other small centric diatom aggregate which includes S. hantzschii. These diatoms were present in the phytoplankton of both the river and the reservoir for most of the period of this investigation. However, it is clear from table 13 that these diatoms were capable of survival in silt (kept in the refrigerator) for at least 24 months (the duration of this experiment). There was probably a much larger initial inoculum of these cells in the silt, than that for either the larger celled Stephanodiscus or for Coscinodiscus so that it is difficult to assess whether there is a real difference in their capabilities to survive at the bottom of the reservoir. It is possible that this difference is merely a reflection of the size of the inocula in each silt sample.

The occasional presence in silt samples of filaments of Melosira which appeared to be 'resting stages' and the frequent occurrence of both Melosira varians and M. granulata in the silt cultures suggested that this was the main method of perennation. However, since neither species was observed in large quantities in the reservoir phytoplankton, but occurred more often in the 'benthic' or 'periphytic' flora, it is possible that auxospore formation was the more important mode of perennation.

Lund (1965) includes both Asterionella and Fragilaria in the group of planktonic algae with no known resting stages. It is interesting to note that neither Asterionella formosa nor Fragilaria crotensis were ever observed in the silt samples or cultures. Only empty frustules of these species appeared to "survive" in the silt. This is confirmed by the work of Lund (1949) on Asterionella formosa that the bottom deposits are unlikely to be a source of inoculum for this species. However, other Fragilaria spp. (one of which was possibly F. capucina) did develop in the silt cultures, and occasionally small filaments of cells with oil bodies and reduced cell contents were observed in the silt samples. It seems likely that these species were also capable of perennation by 'physiological resting stages'. Flint (1949) reported the ability of several species of algae to perennate in the mud deposits at the

bottom of Barn Elms reservoir and included Fragilaria capucina, Nitzschia acicularis, Scenedesmus spp., Coelastrum microsporum and Anabaena spp., in the list. There was apparently less conclusive evidence for the persistence of Pediastrum spp., Closterium, Synedra, Melosira granulata, Aphanizomenon and Fragilaria crotensis. Rao (1953) also cultured samples of pond-silt but there was no attempt made to distinguish the possible methods of perennation.

The apparent absence of Tribonema spp. in river plankton and yet their abundance in the reservoir phytoplankton, suggests the bottom deposits as a possible source of inoculum. Although spore formation has been described in this genus, this was not observed in the reservoir, during this investigation. However, on only one occasion was Tribonema observed in silt cultures and then only a few filaments were present. Flint (1949) noted that Tribonema monochloron was common in culture of silt in either distilled or reservoir water. While it seems most unlikely that these species cannot survive in bottom deposits, the present evidence suggests that the deposits do not appear to be the main source of inoculum. Although there is possibly a long lag period before spore germination which is not covered by this experiment, it is also possible that the main inoculum is derived from cells and filaments persisting in the phytoplankton. In most of the net hauls which were taken during this investigation, Tribonema was observed



although it was frequently absent from the phytoplankton counts.

Lind (1940) suggested that in ponds where the resting stage of most algae would be spent in the mud, the growth of these algae in plankton would depend largely on the extent of subsequent germination of these stages. Similarly Transeau (1913) considered the periodicity and the dominance of different species was associated with the germination of spores. However, in the unstable environment such as the Q.E.II reservoir in which there is a continual throughput of water, the ability of phytoplankton algae to survive in bottom deposits ensures their continued existence in an otherwise rapidly changing system. Although other environmental factors, including turbulence, illumination and nutrients will ultimately determine their importance as phytoplankters in subsequent annual cycles, these species of algae must be considered to have a distinct competitive advantage over other species which are casually introduced from an external source. It is, perhaps this competitive advantage which also, gives a degree of stability (i.e. predictability) to the seasonal pattern of succession in the reservoir (see page 158).



Summary

1. Phytoplankton of the River Thames and the Queen Elizabeth II reservoir has been determined qualitatively and quantitatively during the period November 1965 to May 1968 while culture and laboratory experiments were continued until July 1969.
2. Physical and chemical environmental factors were recorded during the same period and their influence on dominant and sub-dominant members of the phytoplankton flora is discussed.
3. An attempt has been made to compare different methods of determining and expressing the biomass of phytoplankton. These methods included an investigation into the suitability of an electronic particle counter - the Coulter Counter.
4. Of the physical conditions considered, it is concluded that the influence of artificially imposed turbulence - a condition unique to the Queen Elizabeth II reservoir - is probably of prime and possibly over-riding importance in relation to phytoplankton increase and growth. Weak turbulence allows, at least, incipient thermal stratification while vigorous turbulence, although

resulting in isothermality, may at times, by the maintainance of diatoms in suspension for example, encourage phytoplankton growth. On balance, however, the overall influence of imposed turbulence in the new reservoir has, so far, maintained a situation of relatively low population densities distributed through the depths. with regard to the water quality for supply purposes it is clearly necessary to continue surveillance of the phytoplankton in relation to imposed turbulence patterns and the 'ageing' of the reservoir.

5. The importance of the River Thames influent both in relation to water chemistry and the inoculum of phytoplankton, is emphasized.
6. Results of routine analyses indicate that it is probably that the major nutrients, apart from silica, are never limiting to phytoplankton growth in either the River Thames or the Queen Elizabeth II reservoir. The results of culture experiments support the conclusion that silica may at times approach a limiting concentration for the growth of diatoms.
7. Experiments on potential growth rates indicated light limitation in the reservoir during the early spring months.
8. Culture experiments with silt from the reservoir bottom indicated perennation of morphologically undifferentiated

cells of certain centric diatoms, especially Coscinodiscus  
-discus rothii and Stephanodiscus astraes.

9. The validity of results obtained with the Coulter Counter has been investigated and it is concluded that this method of biomass determination is acceptable provided certain elementary precautions are observed and comparisons are made, at least initially, with results obtained by traditional methods (see Appendix 2 . . . Copy of Evans and McGill, 1969).

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# Appendix 1

## Table A

### Oxygen Deficits during August-December 1966 and June-October 1967

1966 Week	Expected Sat.	Observed Sat.	Oxygen Deficit	Relative O <sub>2</sub> Def.	1967 Week	Expected Value	Observed Value	Oxygen Deficit	Relative O <sub>2</sub> Def.
33	9.05-9.4	7.5-8.9	0.1	-	20	10.1-10.8	8.5-8.6	1.5	-
34	9.2-9.5	5.8-10.3	+1.1	1.2	21	10.4	8.0-8.2	2.2	-0.7
35	9.3-9.4	6.4-7.3	2.0	-0.9	22	10.1-10.4	6.65-6.6	1.5	+0.7
36	9.3-9.4	6.6-7.2	2.1	+0.1	23	9.7-10.2	7.15-8.7	1.0	+0.5
37	9.3	6.6-7.0	2.3	-0.2	24	9.7-9.9	7.1-8.05	1.6	-0.6
38	9.4	7.2-8.3	1.1	+1.2	25	9.6-9.7	7.5-8.05	1.5	+0.1
39	9.5	-	-	-	26	9.5	6.55-6.85	2.6	-1.1
40	9.6	6.8-7.1	2.5	-1.4	27	9.4	7.0-7.4	2.0	+0.6
41	9.7	6.9-7.2	2.5	0	28	9.1-9.5	7.3-7.5	1.6	+0.4
42	9.8	7.4-7.5	2.3	+0.2	29	8.8-8.9	7.75-8.1	0.7	+0.9
43	10.1	7.8-7.9	2.2	+0.1	30	8.9	6.95-7.75	1.3	-0.6
44	10.4	10.4-10.7	+0.2	+2.4	31	8.9	7.6-8.4	0.5	+0.8
45	10.8	-	-	-	32	9.0	7.0-7.2	1.8	-1.3
46	-	-	-	-	33	9.1	6.9-7.2	1.9	-0.1
47	11.45	10.0	1.4	-1.6	34	9.1	6.9-7.5	1.6	+0.3
48	11.6	10.5-10.7	0.9	+0.5	35	9.0-9.1	6.0-7.7	2.3	-0.7
49	11.88	11.4-11.5	0.3	+0.6	36	9.1-9.2	7.2-7.7	1.4	+0.9
50	11.88	10.0-10.9	1.0	-0.7	37	9.4	7.9-8.1	1.3	+0.1
51	12.03	11.0-11.1	0.9	+0.1	38	9.5	7.0-7.1	2.4	-1.1

1966 Week	Expected Sat.	Observed Sat.	Oxygen Deficit	Relative O <sub>2</sub> Def.	1967 Week	Expected Value	Observed Value	Oxygen Deficit	Relative O <sub>2</sub> Def.
52	12.03	10.7-11.0	1.0	-0.1	39	9.6	7.5	2.1	+0.3
					40	9.8	7.4-7.5	2.3	-0.2
					41	9.8	8.2-8.7	1.1	+1.2
					42	10.0	8.8-9.8	0.2	+0.9
					43	-	-	-	-

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An investigation of the Coulter Counter in "biomass"  
determinations of natural freshwater phytoplankton populations

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Introduction

The quantitative determination of phytoplankton is a fundamental requirement of almost all studies of the aquatic environment and is especially necessary when production aspects are being investigated. The classical method of visually counting algal units, whether these are cells, colonies, filament lengths or other units appropriate to the size and morphology of the species being studied, is well established (see Lund and Talling, 1957) and is widely used. The results obtained may be expressed in terms of algal units per ml, or other standard volume of the medium, or translations may be made into terms of total algal volume per ml or total cell surface area per ml. The advantage of this procedure is that mixed phytoplankton populations can be considered as a whole instead of species by species. Paasche (1960) interpreted his results as indicating that total cell surface area gives a better estimate of phytoplankton production than does total cell volume but more recent studies (Mullin, Sloan and Eppley, 1966) suggest that although there is an inconstant ratio between cell carbon and cell volume there is a more precise relationship between these two parameters than between cell carbon and cell surface area. The method of microscopical counting, combined with calculation of the total algal volume, if used with care, can lead to valid and acceptable results. Provided only a few species have to be considered this method need not be unduly time-consuming. If, however, many species of diverse shapes and sizes are present and if large numbers of samples have to be dealt with, it can become laborious and cumbersome. The Coulter Counter provides an alternative method for the quantitative determination of phytoplankton which in these situations seems likely to be of great value. In brief, the counter operates by electronic sensing and counting of the number of particles in a suspension in a dilute electrolyte as they pass through a standard aperture. The diameter of the aperture may be varied, by the use of different aperture tubes, so that the overall size range of the particles being counted may be varied

within wide limits. Control settings on the instrument allow the selection of wider or narrower size ranges within the overall range: thus not only numbers, but size distributions of algal populations may be determined.

The Coulter Counter has been successfully used in size determinations of phytoplankton in culture (El-Sayed and Lee, 1963; Mahoney, Donovan and Robinson, 1962) and to a limited extent, of mixed, but usually rather simple, populations from the sea (Cushing and Nicholson, 1966; Parsons, 1965) and freshwater (Mulligan and Kingsbury, 1968). This most recent account makes comparisons of results obtained with an electronic particle counter, with those of biomass determinations by dry weight and chlorophyll-a analyses. However, as a 100 $\mu$ m aperture tube was used throughout all the larger algae (vol. ca.  $6 \times 10^3 \mu\text{m}^3$ ) were missed. It is, nevertheless, an interesting account and confirms our view that the electronic particle counter, in conjunction with other methods, can be used to obtain valid results rapidly. There are also interesting parallels between certain procedural aspects described by Mulligan and Kingsbury (1968) and those arrived at quite independently in this department during 1965-1966. We have both concluded, for instance, that a 0.5% NaCl solution represents the best electrolyte for determinations of freshwater phytoplankton populations.

No records are known of the use of the Coulter Counter in dealing extensively with samples of mixed freshwater phytoplankton. In November 1965 a Coulter Counter model A was loaned to us for a long-term investigation of its use in phytoplankton determinations. Brief preliminary reports were made in January 1967 to the British Phycological Association (Evans, 1967; McGill and Evans, 1967) and a further account was presented in March 1968 to the sixth Coulter Counter Users' Conference in London, England. Our aim here is to report more extensive comparisons of determinations of algal populations, obtained with the Coulter Counter and other methods, as they relate to a variety of natural situations. The accuracy and suitability of the Coulter Counter to any other specific situation may thus be more readily assessed.

The main bodies of water investigated during 1966, 1967 and 1968 were a small, semi-natural lake, on the Surrey-Berkshire border, known as Virginia Water, and the Queen Elizabeth II and King George VI reservoirs of the Metropolitan Water Board. Additional samples were taken also from small local ponds, other reservoirs and the River Thames. The phytoplankton of Virginia Water is the subject of long term investigation, since 1958, by one of us (J.H.E.). This lake is about one kilometre long in its east-west



axis, about 400 metres wide and three metres deep. There are several main inflows but only one outflow via an outlet stream and small waterfall at the eastern end from where most samples have been taken. The water is eutrophic and the concentrations of major anions are usually relatively high ( $\text{PO}_4\text{-P}$ , 3-50  $\mu\text{g/L}$ ;  $\text{NO}_3\text{-N}$  0.03-1.68 mg/L;  $\text{SiO}_2$ , 0.3-15.4 mg/L) (See<sup>4</sup> Evans, 1964). Over the past ten years the annual phytoplankton succession has been generally one of spring and autumn diatom maxima with late summer growths of Cyanophyceae between. The Queen Elizabeth II reservoir which was completed in 1963, is a through-put, supply reservoir, with a controlled inflow from the River Thames of 30-120 million gallons a day via conventional bellmouth inlets or a shoreline system of jets to entrain water and ensure turbulence. The surface area is about 317 acres (128 hectares), the maximum depth is 17.5 metres and the capacity about 4300 million gallons. The King George VI reservoir was completed in 1949 and is a standing reserve of about 4500 million gallons with a surface area of about 350 acres (142 hectares) and a maximum depth of 16 metres. The concentration of major anions in these reservoirs largely reflects their concentration in the River Thames and indicates high eutrophy ( $\text{NO}_3\text{-N}$ , 1-6 mg/L;  $\text{NH}_4\text{-N}$ , 0.1-1.1 mg/L;  $\text{NO}_2\text{-N}$ , 0.008-0.1 mg/L;  $\text{PO}_4\text{-P}$ , 0.46-2.0 mg/L;  $\text{SiO}_2$ , 2-17 mg/L). The reservoir phytoplankton succession is somewhat similar to that of Virginia Water but often includes the occurrence of marked summer growths of *Tribonema* and is influenced strongly by the particular patterns of input from the River Thames and, especially for the Queen Elizabeth II reservoir, imposed turbulence.

### Methods

From Virginia Water, outlet samples were collected, usually in duplicate or triplicate and at weekly or more frequent intervals, in 500 ml polythene bottles and returned to the laboratory within the hour for analysis and preservation. From the reservoirs, samples were collected with a Friedinger sampler from a boat. From the Queen Elizabeth II reservoir, some samples were preserved or used for chemical analyses almost immediately in the Metropolitan Water Board laboratory at Walton while fresh samples were returned to the Royal Holloway College Botany Department and either analysed immediately or formalin preserved and refrigerated overnight before particulate matter determinations the next day. Samples from the King George VI reservoir were usually analysed on the day of their collection. Phytoplankton was preserved by the addition of a mixture of iodine, potassium iodide and glacial acetic acid (in the proportions: I, 10 gm; KI, 20 gm; acid, 20 ml; distilled water, 200 ml) so that the final colour of the preserved sample was rich, red-brown. All microscope counts were by the iodine

sedimentation/inverted microscope technique with the modification that a split sedimentation tube was employed to allow the use of high-power, including oil-immersion, objectives where required.

After calibration with Lycopodium spores and many preliminary experiments with uni-algal cultures (e.g. Cosmarium botrytis (Bory) Menegh., Carteria eugametos Mitra, Asterionella formosa Hass.) the Coulter Counter was applied to natural populations as follows: the electrolyte, sodium chloride, was added as a 10% solution to the sample to give a final concentration of 0.5% NaCl in 300 or 400 ml of test sample. The sample temperature was adjusted to 20°C and the sample was stirred constantly during analysis. A 200  $\mu\text{m}$  aperture tube, which deals with particles in a volume range of about 50-120,000  $\mu\text{m}^3$  was used almost throughout and the manometer volume control set at 0.5 or 2 ml depending upon the concentration of particles in the suspension. From the calibration values a series of up to sixteen instrument settings were derived which related, for the main part of the investigation, to particle volumes from which further calculations could be simply made. Coincidence corrections were made for particle concentrations exceeding 400 units per 0.5 ml of the test suspension. Results were listed in prepared blank tables, the results being set out under the following headings:-

N = total particle count per 0.5 or 2 ml (mean of 2 or 4 particle counts, with coincidence correction);

V = minimum particle volume in  $\mu\text{m}^3 \times 10^3$  at each setting;

$\Delta N$  = particle number per 0.5 or 2 ml within each volume setting;

$\Delta NV$  = total particulate volume in  $\mu\text{m}^3 \times 10^3$  per 0.5 or 2 ml within each volume setting;

$\Sigma \Delta NV$  = total particulate volume (T.P.V.) above any selected volume setting, usually transformed into terms in  $\mu\text{m}^3 \times 10^3$  per ml or  $\mu\text{m}^3 \times 10^6$ /ml.

In this way, total particulate volumes (T.P.V. in figures) per ml of sample after a simple calculation could be selected from any desired size range represented in the table - a glance at the N column indicating any distinctive population of particles of any particular size range.



Some phytoplankton algae in their naturally occurring form are clearly unsuitable for size analysis with the Coulter Counter. Long filaments of large cells, for example, may tangle together and block the aperture. It was found necessary to reduce such algae to a more manageable form and for this purpose use was made of a Maxomatic ultrasonic shaker. This was found for example, in combination with a dilute solution of pectinase and manual stirring to separate long filaments of Tribonema vulgare Pasch. into lengths of 2-4 cells, units which could then be sized and counted with the Coulter Counter. Manual shaking alone was found to be a better method of dispersion for some algae. Colonies of coccoid Cyanophyceae, such as Microcystis flos-aquae (Wittr.) Kirchn., sometimes were and sometimes were not separated into individual cells by the ultrasonic technique while manual shaking was sufficient to separate colonies small enough to be sized and counted with the 200  $\mu$ m aperture tube.

For comparison with the Coulter Counter results, calculated algal volumes were derived from measurements of not less than 100 cells or other units and by the assumption that these approximated in shape to regular solids. Dry weight of particulate matter was determined on glass-fibre filtered samples dried at 40°C and particulate carbon was determined by the wet oxidation method with dichromate. For the Queen Elizabeth II reservoir and River Thames samples, pigments were extracted with a mixed solvent (methanol, ethanol, propanol, ether and acetone in equal parts) overnight at about 0°C. Then, after transference to methanol, the pigment concentration was determined in a 1 cm cell on an SP 500 Unicam spectrophotometer. Chlorophyll-a concentration was calculated using the equation of Talling and Driver (1963).

### Results and Discussion

The term biomass is used here in the widest possible sense and is taken as being the amount of algal material present in a specified volume of water at a particular point in time. In agreement with Westlake (1965), biomass is further defined so as to include dead or non-protoplasmic material such as cell walls. Whether algal volume can be used as a valid measure of biomass is arguable. In Westlake's opinion (1965) algal volume is not a good measure of biomass. We have attempted to show here, however, that volume which is the character specifically measured with the Coulter Counter by virtue of its very mechanism, may be used as a suitable indicator of algal quantity.

From the many completed data sheets resulting from the use of the counter only sufficient have been extracted here for interpretive purposes. To illustrate the uses that we have made of this instrument three main approaches are presented:-

1. Particle number and size distribution of phytoplankton samples (Fig. 1);
2. Comparison of total particulate volume (T.P.V.) with one other parameter (Figs. 2, 3, 4, 6, 7);
3. Seasonal changes of T.P.V.s (Figs. 10 and 11) and compared with one (Fig. 8) or more (Fig. 9) other characteristics of natural phytoplankton populations.

The analyses shown in Figure 1 are similar to and broadly comparable with those figures accompanying the paper by Parsons (1965) except that our figure is on a two-way log basis and the size intervals are not so fine as those selected by Parsons. The histograms on the left show two natural, mixed phytoplankton populations from Virginia Water, the lower, unbroken line representing a January sample and the upper, broken line, an April sample, both in 1966. The shaded portions are the particles in the size range, checked by microscope measurements, of Asterionella formosa colonies. In January, there were 60 colonies per ml (mean number of cells per colony  $\sqrt[n]{\text{for } n = 50} = 2.5$ ) which equated with the 60 particles (i.e. colonies) per ml registered with the Coulter Counter in the appropriate size range. In April there were 1,116 colonies per ml (mean number of cells per colony  $\sqrt[n]{\text{for } n = 100} = 4$ ) and this is well within 10% of, and therefore acceptably close to, the 1038 particles (i.e. colonies) per ml registered with the counter. The histogram on the right is of a dense, unialgal culture, diluted by a factor of 20, of Asterionella formosa which originated from the King George VI reservoir of the Metropolitan Water Board; there we see, accompanying the higher density of this species in culture, a closer approach to a normal size distribution than is apparent in the naturally occurring mixed sample of plankton, and a wider size range. At the lowest size bracket occurred single cells of one of the smaller varieties of this species with cells of about  $200\text{-}400\text{ }\mu\text{m}^3$  in volume. The skew to the right is a result of the increase in culture of larger cells ( $800\text{ }\mu\text{m}^3$  or more) aggregated into multi-celled colonies (32 cells or more arranged in a helical form). In Virginia Water in 1966 in addition to the spring growth of Asterionella there was a distinct though small increase in August, to about 2,000 cells per ml. The increase in particulate volume due to the cells of Asterionella however, was partially masked by a rather sudden increase in Microcystis flos-aquae (see Fig. 8).

During the period August to October 1966 Microcystis flos-aquae was the dominant alga in Virginia Water lake and was present, except for the early part of its growth, almost to the exclusion of other phytoplankton algae. Although the colonies were neither precisely regular in shape nor constant in size they almost all approximated to spheres or sub-spheres, due partly to the break-up of larger colonies, and occupied a narrower size range than is usually encountered. Comparisons of visual determinations of colony numbers (Fig. 2) with electronically determined particles/ml (Fig. 2A) and T.P.V./ml (Fig. 2B) indicated close agreement between the different methods of analysis. Such close agreement might not be realised with more irregularly shaped colonies, but these results indicate that the results obtained electronically would alone be sufficiently accurate and reliable for most ecological work. A further point of interest here is that the mean colony size, which may be derived from Figure 2B, of  $10^5 \mu\text{m}^3$  is precisely the same as that reported by Nauwerck (1963).

Similar results, indicating positive correlations between visual and electronic methods of quantitative determination, were obtained for two diatoms [Fragilaria crotonensis Kitton and a centric diatom referred to Coscinodiscus rothii (E) Grun (?=Actinocyclus sp.)] each of which occurred as a dominant alga in mixed natural populations from the Queen Elizabeth II reservoir (Fig. 3).

Within the range of particle size studied ( $50-120,000 \mu\text{m}^3$ ) with the  $200 \mu\text{m}$  diameter aperture tube there was usually a close correlation between T.P.V. and dry weight of sample particulate matter (Fig. 4). A comparison was made in parallel samples of chlorophyll and carbon content (Fig. 5) and these also were found to be positively correlated. However comparisons of chlorophyll (Fig. 6) or calculated algal volumes (Fig. 7) with T.P.V. did not indicate simple linear relationships throughout the concentration range which occurred in natural samples. Especially in the reservoir, the non-algal suspended matter at times formed a high proportion of the total. These results clearly indicate, however, that above a T.P.V. value of about  $0.8 \times 10^6 \mu\text{m}^3/\text{ml}$  the Coulter Counter determinations do reflect algal volume and chlorophyll content of the phytoplankton in mixed natural populations.

This method of electronic determination has been applied to many situations in nature to investigate its potential as a tool for regular routine use in phytoplankton investigations. A few examples of our investigations follow:



Virginia Water lake represents a complex biological situation of a eutrophic water showing wide fluctuations in chemistry and in the phytoplankton populations. Figure 8 which represents a highly simplified version of the real situation shows the seasonal changes in algal numbers compared with the T.P.V. results during 1966-68. Except for the first sample recorded here, in January 1966, and a few later samples, the T.P.V. exceeded  $10^6 \mu\text{m}^3$  throughout so that the fluctuations are likely to have reflected changes in the algal biomass from time to time. Visual determinations of algae, qualitatively and quantitatively, support this conclusion. In this figure, only the dominant algae are recorded and as they have been recorded numerically, in cells or other units/ml, the different species are not strictly comparable one with another. However, it is clear that the T.P.V. results do parallel the changes in phytoplankton quantities and, what is more, simplify seasonal comparisons. The dense bloom of Microcystis flos-aquae of the late summer to autumn, 1966, for example, is correlated with the maximum T.P.V. results during 1966-67. As a comparison, high cell numbers of the flagellate Cryptomonas, although associated with T.P.V. peaks in the spring of 1967, fell far short of the total biomass of Microcystis of the previous autumn.

In Fig. 9 there is a comparison of four parameters, dry weight, carbon, calculated algal volume and T.P.V. during 1966-67 in the Queen Elizabeth II reservoir. Again, it is clear that the results attained by the different methods are broadly comparable even though the lower T.P.V.s recorded are close to, and some are less than, the critical value of  $0.8 \times 10^6 \mu\text{m}^3/\text{ml}$ .

As a further example of the use of T.P.V. in recording phytoplankton biomass, Fig. 10 is derived from results obtained from the King George VI reservoir during parts of 1967 and 1968. In addition to seasonal changes this figure indicates vertical distribution. In early July 1967 and from mid October 1967 to late February 1968 the T.P.V. for all samples was lower than  $0.8 \times 10^6 \mu\text{m}^3/\text{ml}$  so that any differences in phytoplankton concentrations were probably masked by detritus. The T.P.V. increase in July - early August, although suggesting an increase in biomass, is probably an under valuation. Events which occurred during this period included the appearance and growth of planktonic algae such as Fragilaria crotonensis, Eudorina elegans and Pediastrum duplex, a great increase in oxygen production in late July and in chlorophyll

concentration in early August. The oxygen and chlorophyll results were supplied by Mr. A. Steel of the Metropolitan Water Board. It is likely that the large colonies of Pediastrum, which reached maximum concentration in early August, were missed in the Coulter Counter determinations. In March 1968 a great increase of plankton diatoms occurred and this is well reflected in the T.P.V. results. This increase was due largely to centric diatoms, including Stephanodiscus astraea and high numbers of other, small centric diatoms, which were carried in with River Thames inflow water. From late February the inflow rate was at about 100 million gallons per day until late in March when this was stopped. The subsequent T.P.V. increase suggests some growth in the reservoir, and the vertical pattern indicates sedimentation through April. The apparent overall decrease by late April is likely to have been due to the settlement of these diatoms to the bottom of the reservoir.

As a final illustration we present T.P.V. results comparing the Virginia Water lake phytoplankton and that of a small pond in 1967 (Fig. 11). The floral compositions of these two bodies of water are quite unlike and qualitatively distinct from one another. In the lake there is a more or less complex assemblage of many species of phytoplankton algae dominated at times by diatoms and at others by blue-green algae or flagellates. This is indicated in a simplified fashion in Fig. 11. The pond flora during 1967 consisted of a species assemblage which was qualitatively almost constant and dominated throughout by a small desmid, Cosmarium ref. pygmaeum var. perornatum Skuja.

In phytoplankton biomass, as presented by T.P.V., the pond flora was consistently higher by an order of magnitude, than the lake flora and also showed, except for the autumn decrease, a remarkable constancy compared with that of the lake.

#### Summary and Conclusions

During the period November 1965 to November 1968 an investigation has been made into the use of the Model A Industrial Coulter Counter for determining the biomass of freshwater phytoplankton.

Parallel determinations of other parameters, including algae numbers, calculated algal volumes, dry weight, carbon content and chlorophyll pointed towards the general validity of the results obtained by the electronic method provided the background level of non algal detritus is relatively low.

The importance of parallel determinations, especially those involving visual inspection of samples, is emphasized.

For uni-algal samples, either from culture or nature, or for natural samples dominated by one species, the Coulter Counter does not necessarily give a quicker result than traditional methods of analysis. However, for at least two reasons the Coulter Counter adds a most useful new dimension to the realm of phytoplankton analysis. For assemblages of algae, whether or not certain species are dominant or co-dominant, a more rapid determination of a result, which can be taken to represent the biomass, is possible than by other methods. Such results, expressed here as total particulate volume (T.P.V.), can be accepted as being as accurate as those obtained by any other method and are probably better than some.

In addition to the single figure T.P.V. result for a sample, volume analyses within selected size and particle number ranges can be made.

#### Resume et conclusions

Entre Novembre 1965 et Novembre 1968 une enquete a ete poursuivie sur l' utilisation du Model A Industrial Coulter Counter pour la determination de la biomass des phytoplanctons d'eau douce.

La determination parallele d'autres parametres, tels que les numeros algals, les volumes algals calcules, les poids a sec, le contenu de carbone et la chlorophylle a indique la validite des resultats obtenus par la methode electronique, pourvu que le niveau de detritus non-algal soit relativement bas.

On notera l'importance des determinations paralleles, surtout de celles qui impliquent l'inspection visuelle des echantillons.

Pour les echantillons uni-algals, qu'ils soient naturels ou cultives, et pour les echantillons naturels domines par une seule espece, le Coulter Counter ne donne pas necessairement un resultat plus rapide que les methodes d'analyse traditionnelles. Neanmoins, pour au moins deux raisons, le Coulter Counter ajoute une nouvelle dimension tres utile au domaine de l'analyse des phytoplanctons.



Pour les assemblages d'algues, domines ou non par une ou par plusieurs especes, la determination plus rapide d'un resultat qu'un peut considerer comme representant la biomasse est possible par cette methode que par toute autre. Ces resultats, exprimes ici en volume particulaire total, (T.P.V.), sont aussi exacts que ceux qu'on obtient par toute autre methode. Ils sont meilleurs, probablement, que les resultats donnees par quelques-unes de ces methodes.

En plus de resultat T.P.V. a simple numero pour chaque echantillon on peut faire des analyses de volume dans une gamme donnee de dimensions et de nombres de particules.

#### Acknowledgements

Our grateful thanks are due to Coulter Electronics Ltd. for the loan of a Model A Industrial Coulter Counter and especially to Mr. W.M. Wood and his colleagues of the Dunstable, England, branch for much technical help in its use. Our thanks are also due to Mrs. P. Andrews of the Botany Department of Royal Holloway College for valuable assistance in the use of the machine and in preparation of the figures, as well as to Miss L. Peachey and Miss L. Etherington. The Metropolitan Water Board provided valuable facilities and we are especially grateful to the Staff of the Biology Section. Finally, we thank Professor Wilson for his constructive criticism of the penultimate draft of this paper.

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### Figure Captions

- Fig. 1. Asterionella formosa (shaded portions) in mixed natural populations from Virginia Water lake (left) and in a dense, unialgal culture of colonies derived from the King George VI reservoir (right). Two mixed samples are illustrated, the lower represents that of January and the upper (broken line) that of April 1966, and the results parallel the seasonal increase from about 150 to 4,500 cells per ml. The unshaded portions consist of particles outside the size range of the colonies in these samples. The culture was diluted by  $\times 20$  to attain the analysable concentration illustrated and the figure (right) indicates a much wider range of colony size than occurred in the natural populations (see text).
- Fig. 2. Microcystis flos-aquae - a comparison of colony numbers determined by microscope counts (horizontal scale) with particles per ml (upper figure) and total particulate volume, in  $\mu\text{m}^3$  per ml (lower figure) in the size range  $3 \times 10^4$  to  $1 \times 10^5 \mu\text{m}^3$ , determined with the Coulter Counter, in Virginia Water lake samples of August to October 1966 when this alga was dominant (cf. Fig. 8 and text).
- Fig. 3. Total particulate volumes and calculated algal volumes of reservoir phytoplankton samples dominated by Coscinodiscus rothii (circles) or Fragilaria crotonensis (squares).
- Fig. 4. A comparison of the dry weight of residues on glass fibre filters and the volume of suspended matter determined with the Coulter Counter, from reservoir samples.
- Fig. 5. A comparison of chlorophyll and carbon content of the particulate matter in samples from the Queen Elizabeth II reservoir (o) and the River Thames (o) in 1966-67.
- Fig. 6. A comparison of T.P.V. and chlorophyll in samples from the Queen Elizabeth II reservoir (o) and the River Thames (o) in 1966-67.
- Fig. 7. A comparison of T.P.V. and calculated algal volume in samples from the Queen Elizabeth II reservoir (o) and the River Thames (o) in 1966-67.

Fig. 8. Seasonal changes in the phytoplankton and total particulate volumes (T.P. V.) of outflow samples from Virginia Water during 1966-68. Only the more important algal constituents are represented, diatoms by dotted lines, blue green algae by broken lines, Ceratium by unbroken lines and Cryptomonas by intermittent lines. Except where otherwise indicated all are recorded as cells per ml.

Scale A refers to Melosira varians (O), Synedra ulna ( ), Microcystis flos-aquae (o) (colonies per ml) Cryptomonas ref. curvata (o) and Ceratium hirsutum (O.F. Muller) Schrank ( )

Scale B refers to Melosira granulata (o), Asterionella formosa (o), Diatoma vulgare ( ), Anabaena spp. (o), Aphanizomenon flos-aquae (O), (filament lengths per ml), Cryptomonas ref. ovata (o) and Cryptomonas spp. (mainly C. ref. ovata) (o).

T.P.V. is represented by an unbroken line (o) and almost every sample was collected, determined with the Coulter Counter, and is recorded here in duplicate. The overall sampling and machine errors rarely resulted in duplicate sample differences exceeding 10%.

Fig. 9. Seasonal changes in calculated algal volumes (C.A.V.) (unbroken line), total particulate volumes (T.P.V.) (broken line), carbon (C) (unbroken line) and dry weight of suspended matter (D.W.) (dotted line) in the Queen Elizabeth II reservoir during 1966 and 1967.

Fig. 10. T.P.V. of depth samples from the King George VI reservoir in 1967 and 1968. Depth in metres on the vertical axis. T.P.V. as  $\mu\text{m}^3 \times 10^6/\text{ml}$ . The dark line parallel with the time axis indicates the period of River Thames inflow.

Fig. 11. A comparison of T.P.V.s of Alderhurst pond and Virginia Water lake in 1967.

FIG. 1  
(EVANS AND McGill)

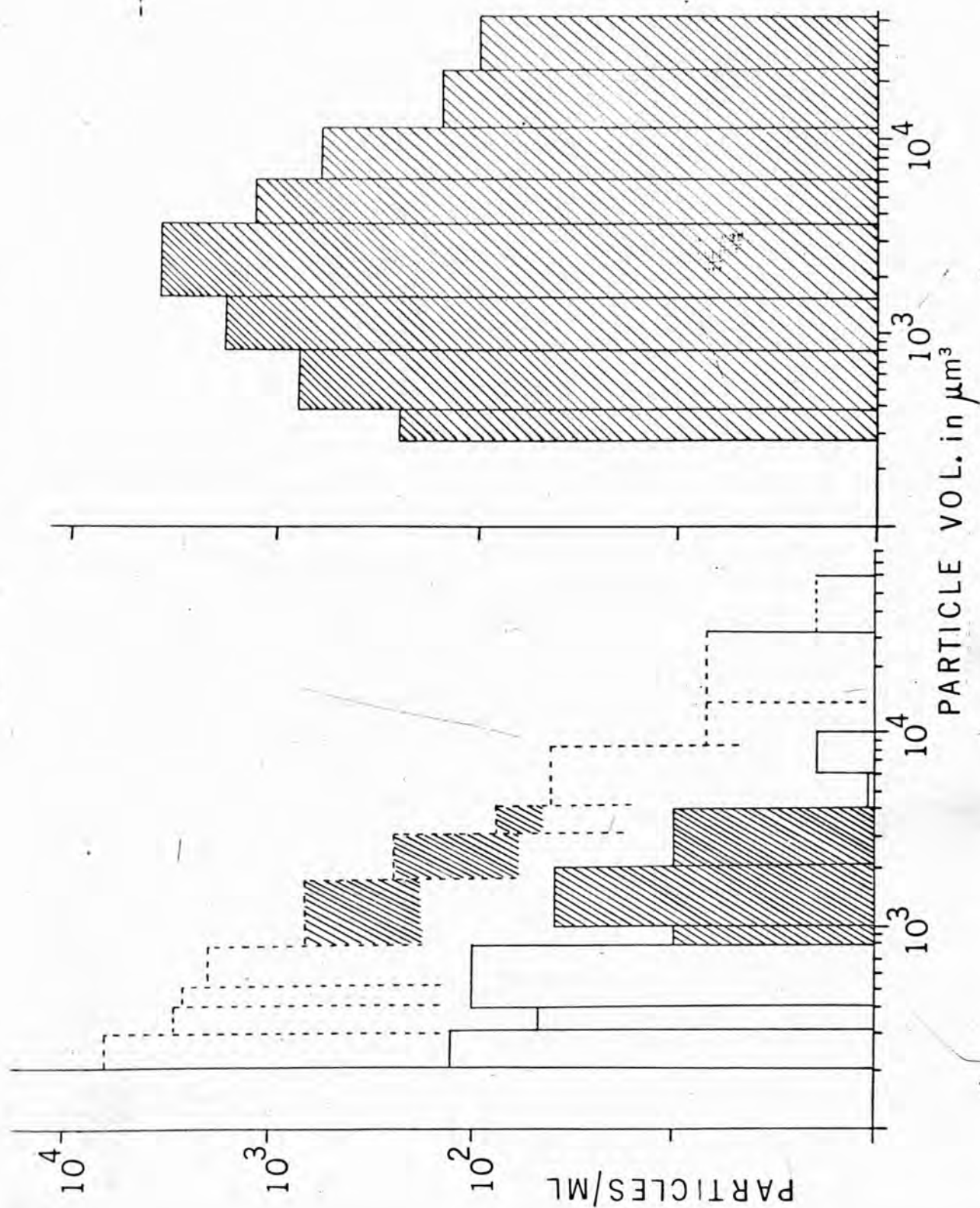




FIG. 2  
(EVANS AND MCGILL)

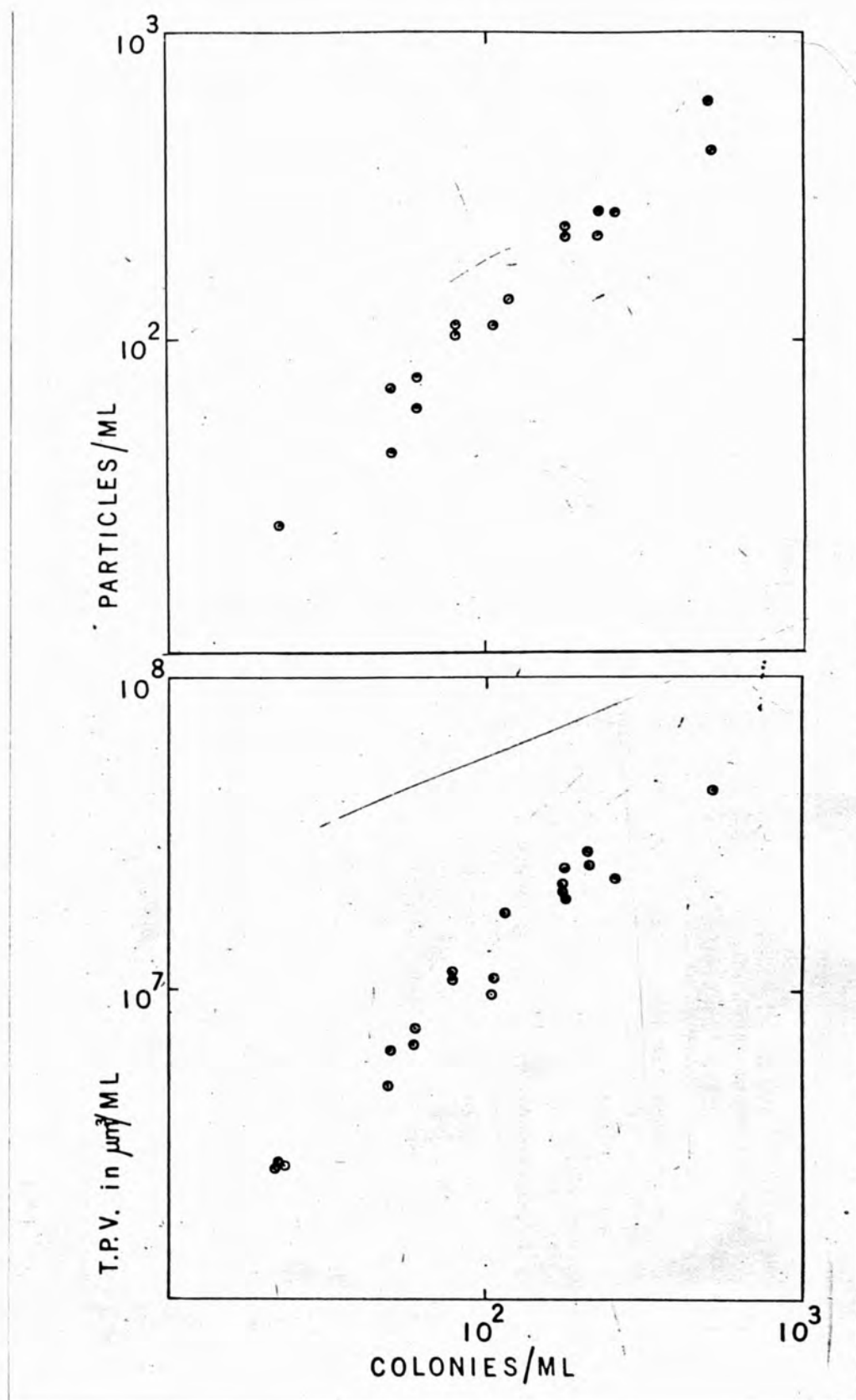
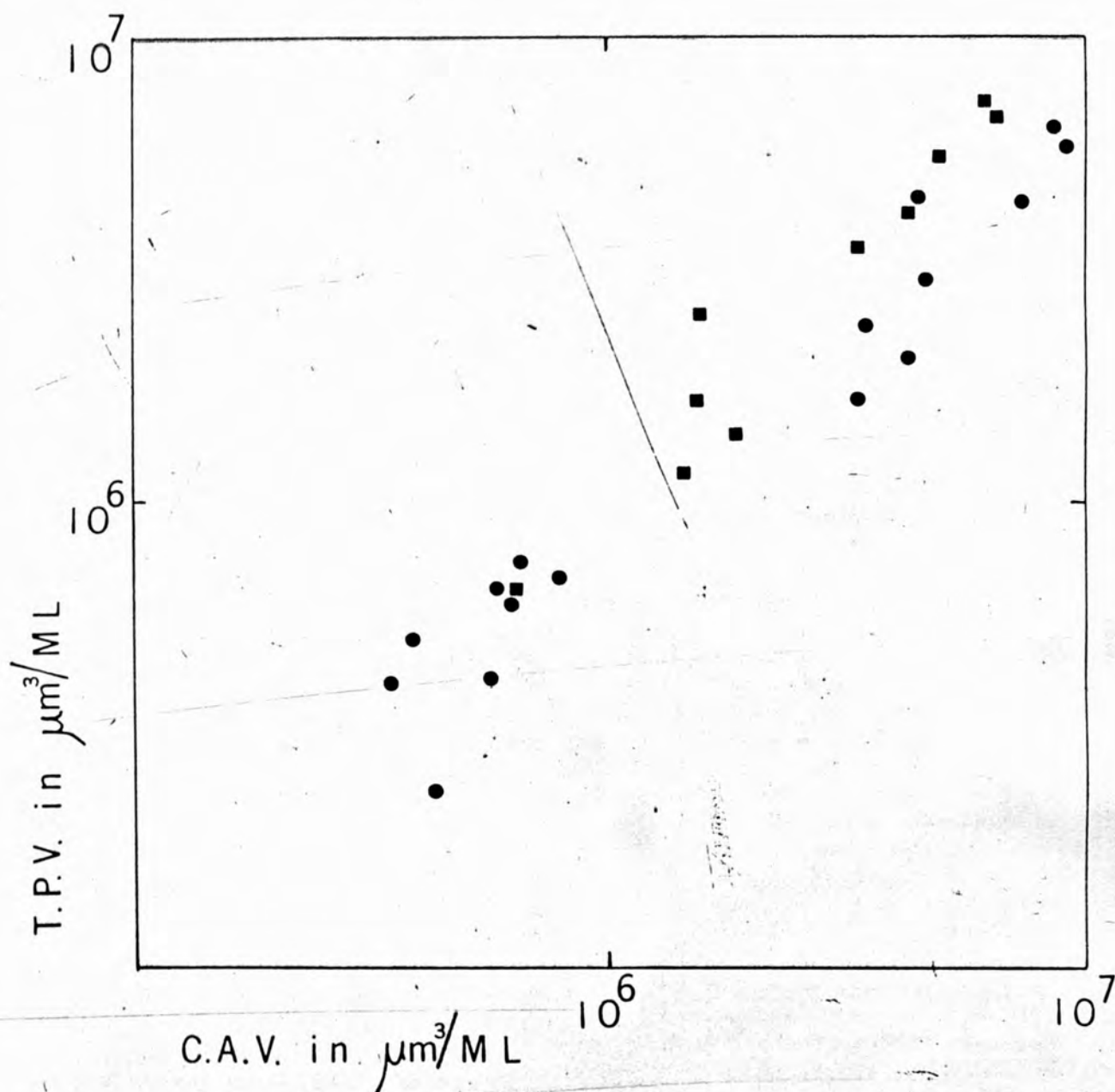




FIG. 3  
(EVANS AND M'GILL)



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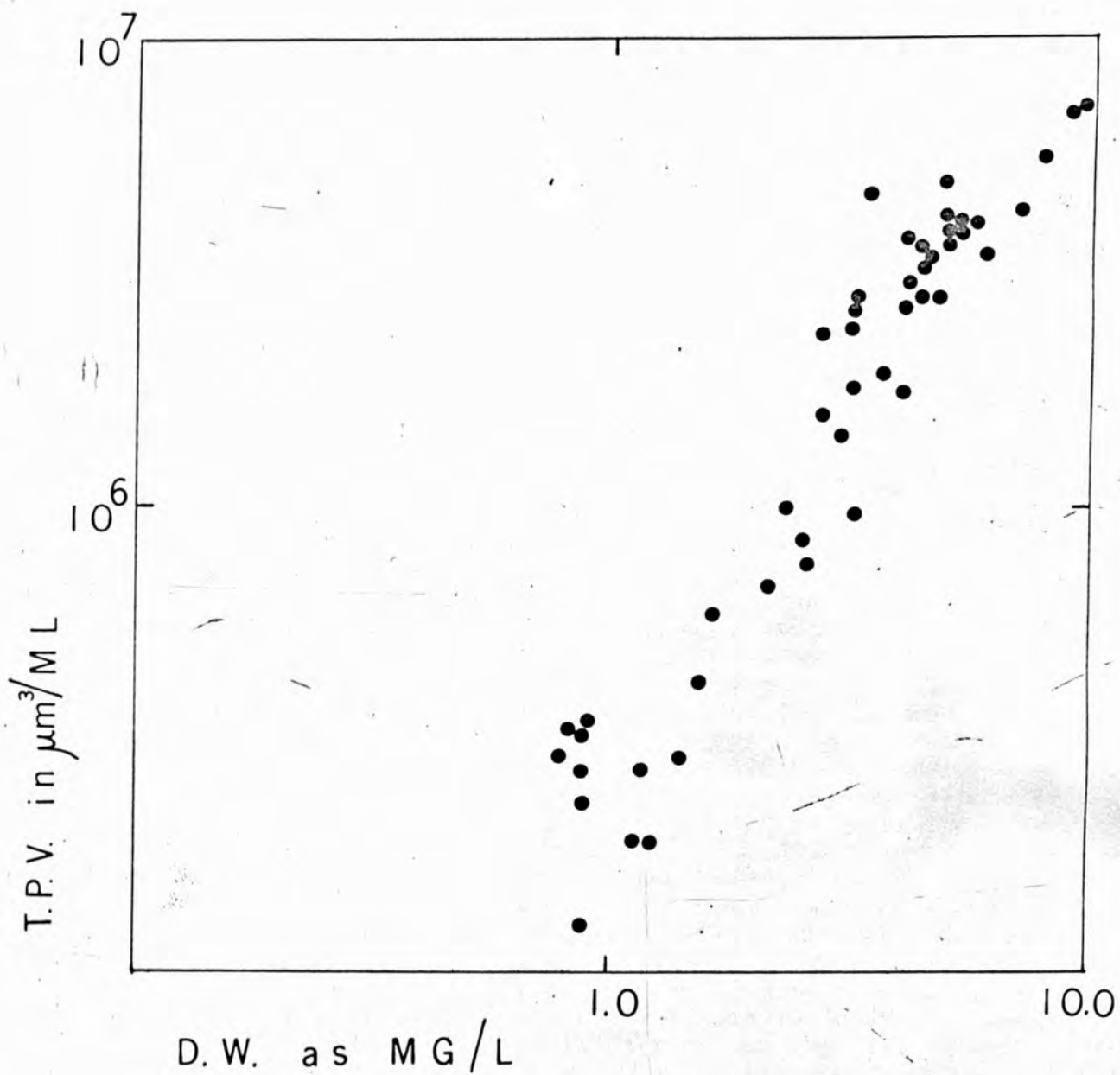


FIG. 5  
(EVANS AND MCGILL)

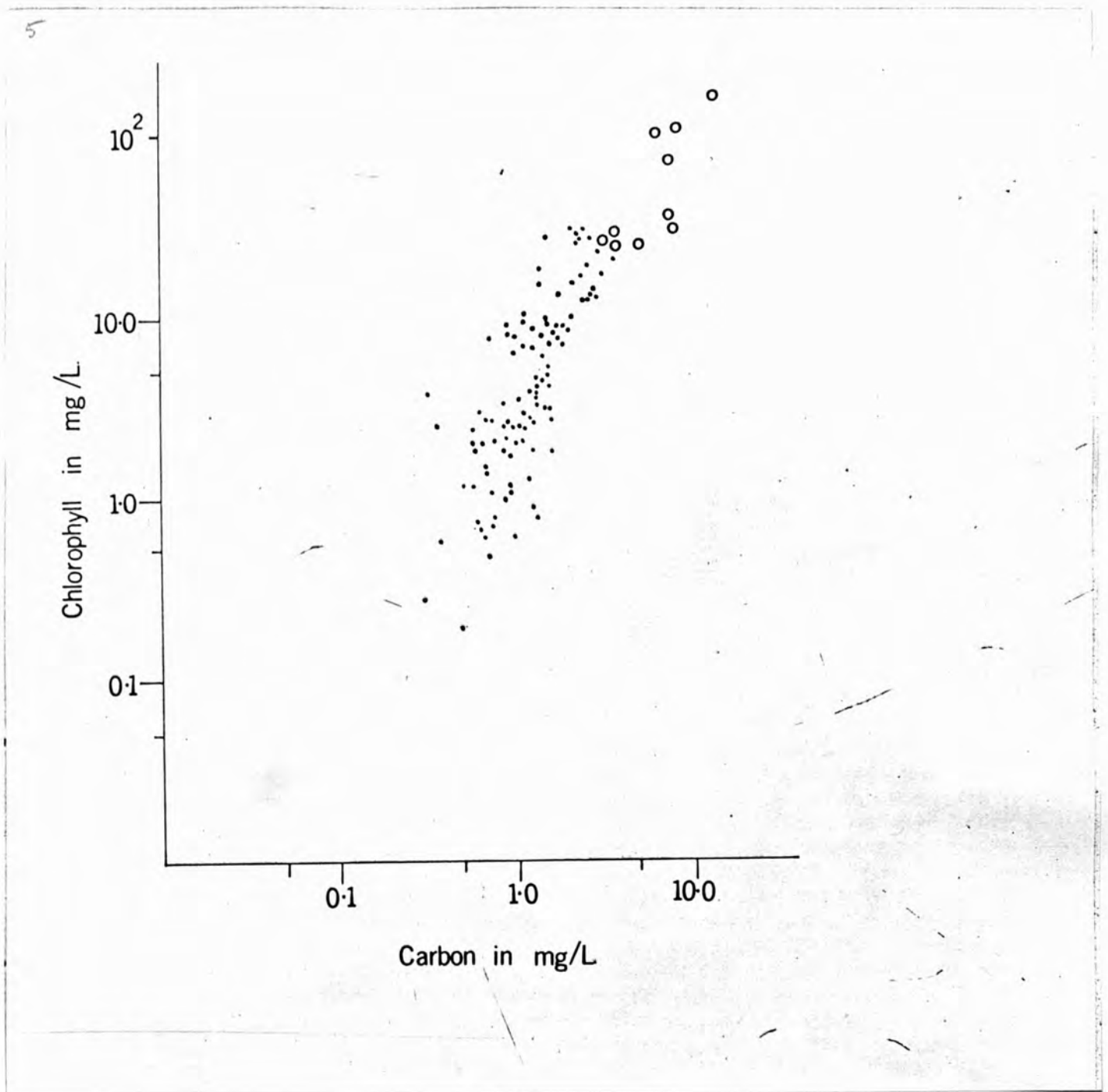


FIG. 6  
(EVANS AND MCGILL)

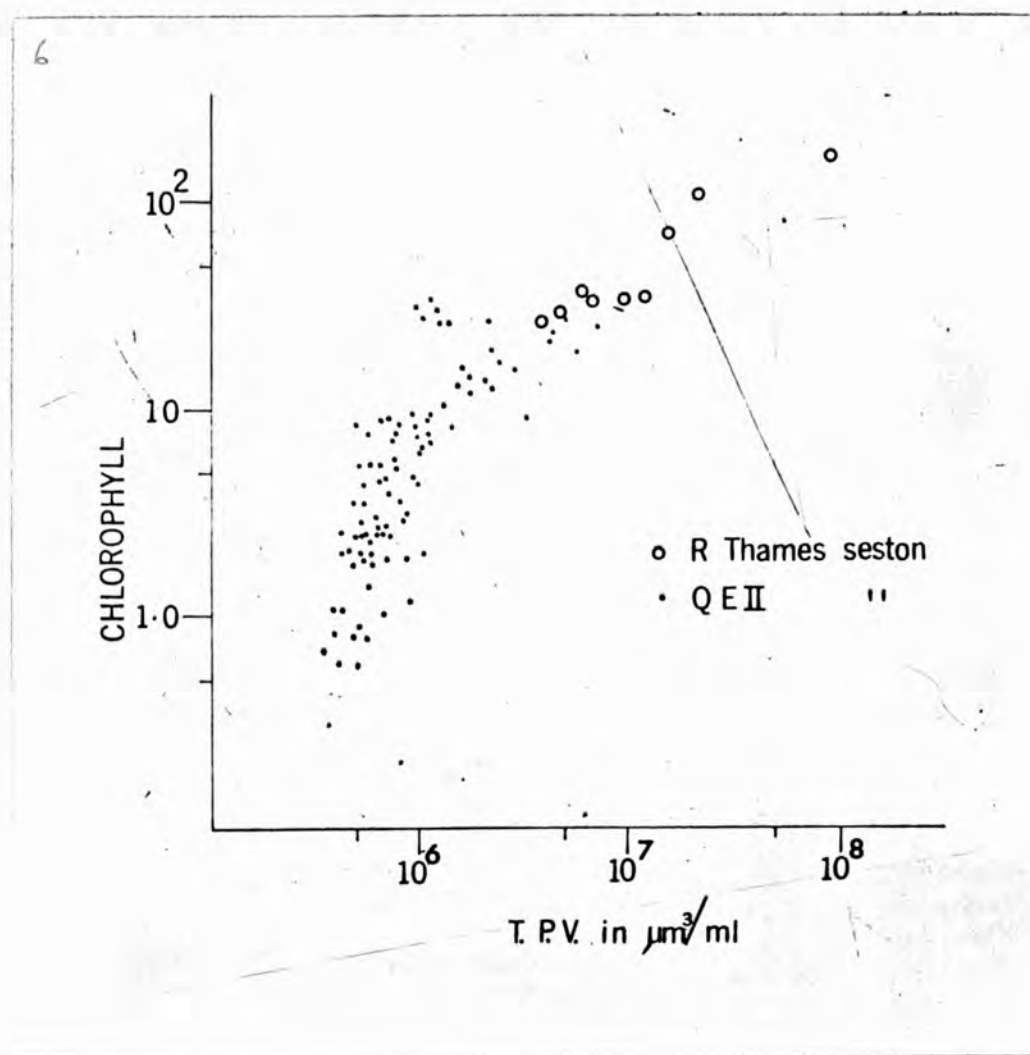


FIG. 7  
(EVANS AND M'GILL)

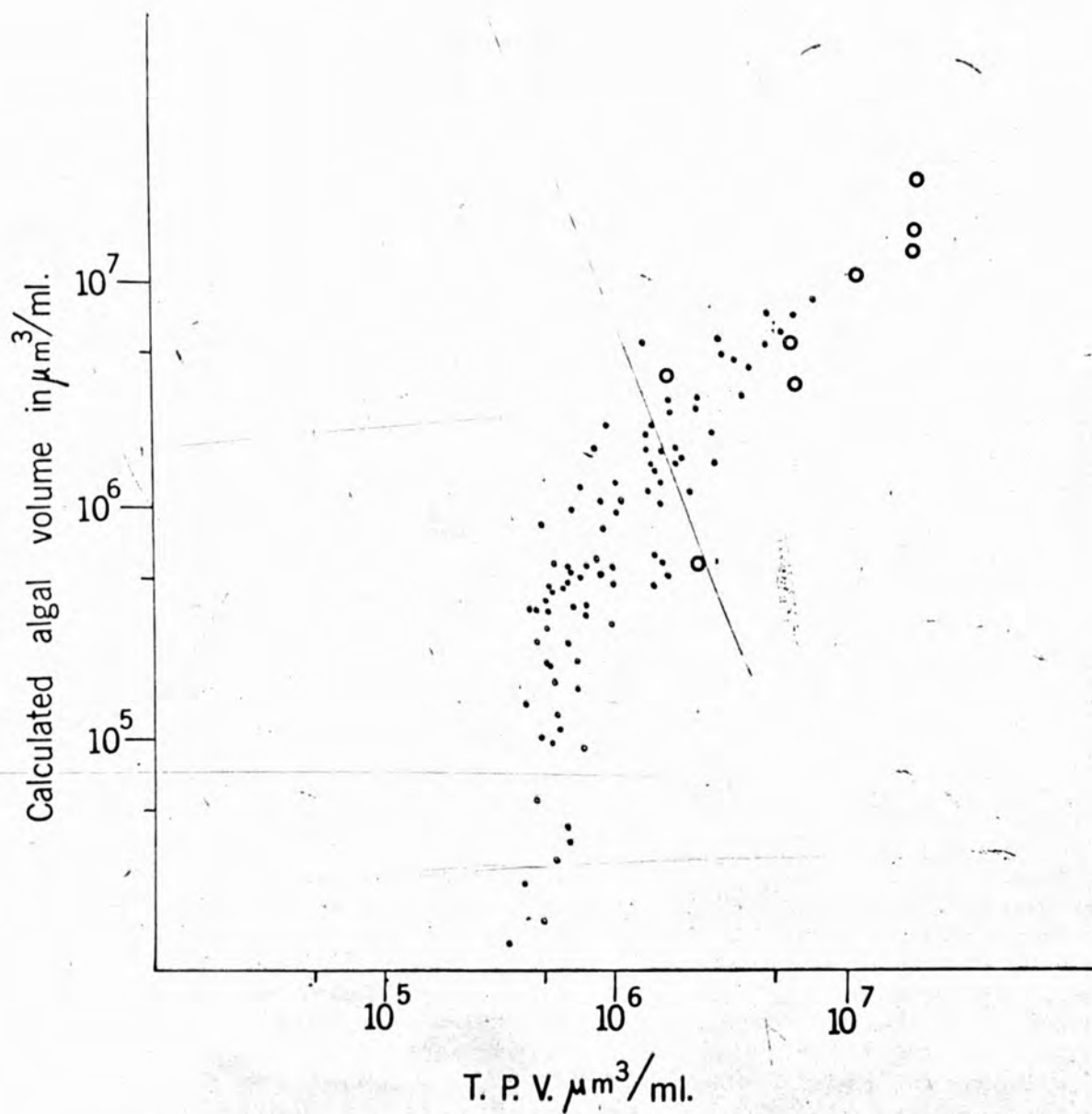
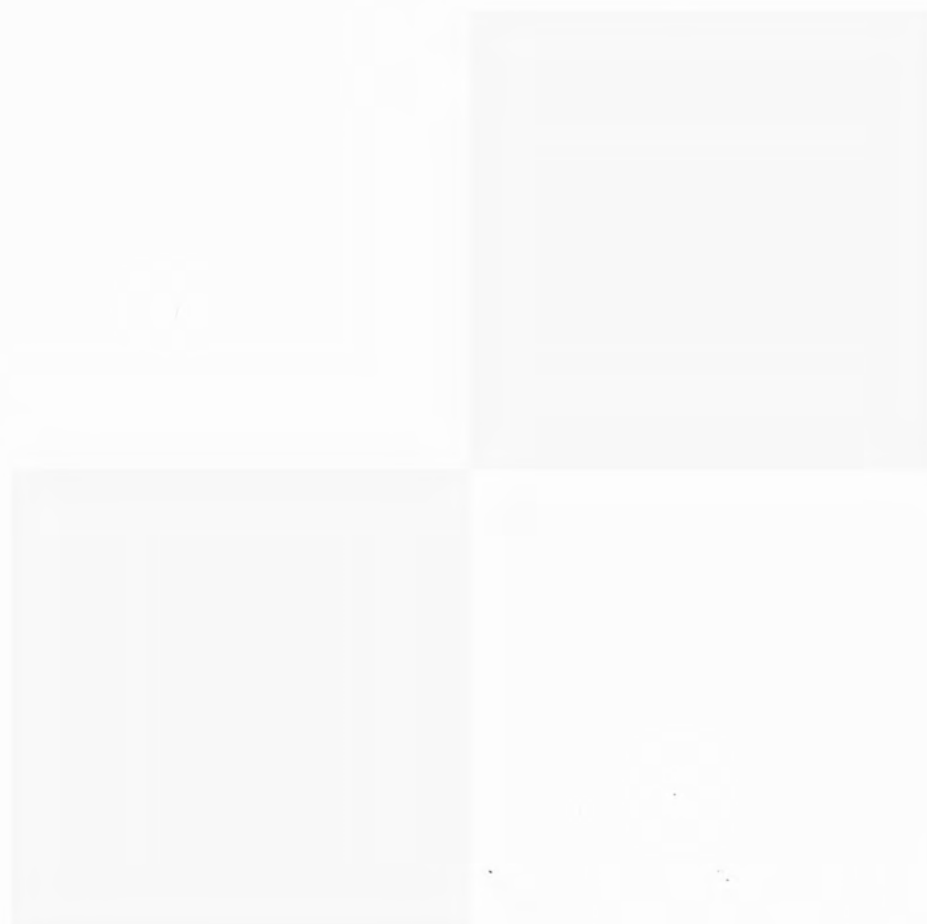


FIG. 8

EVANS AND MCGILL





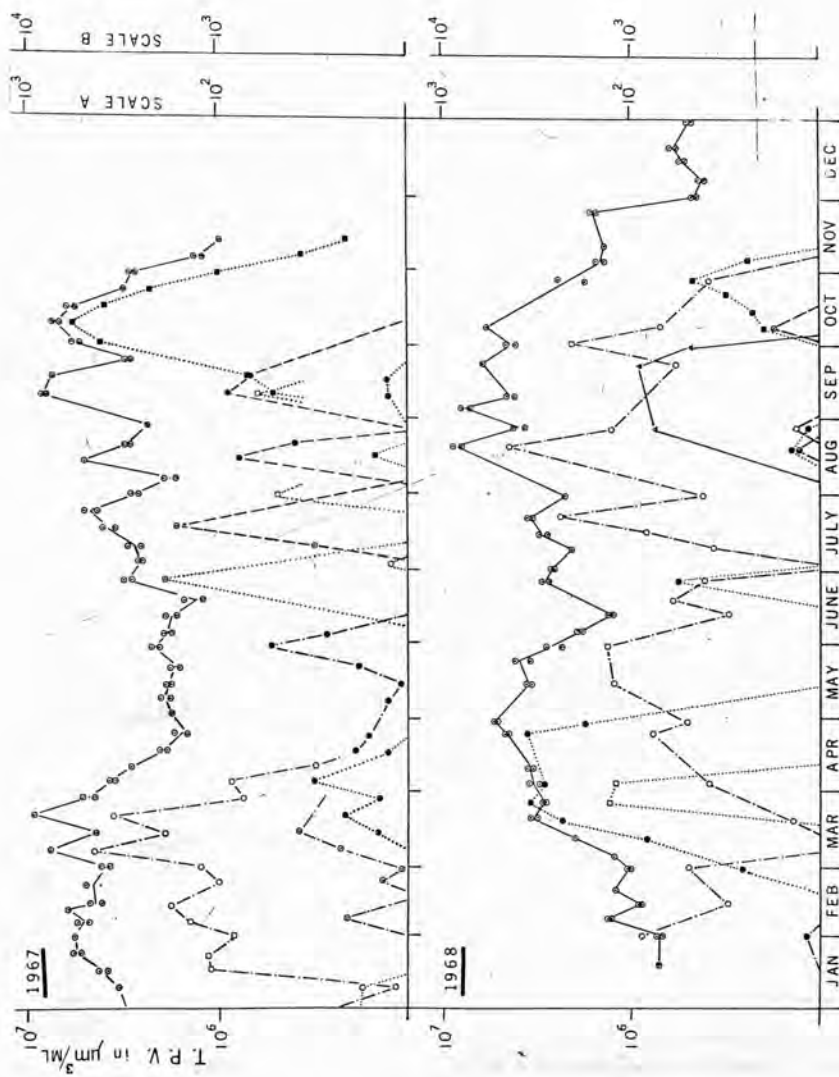
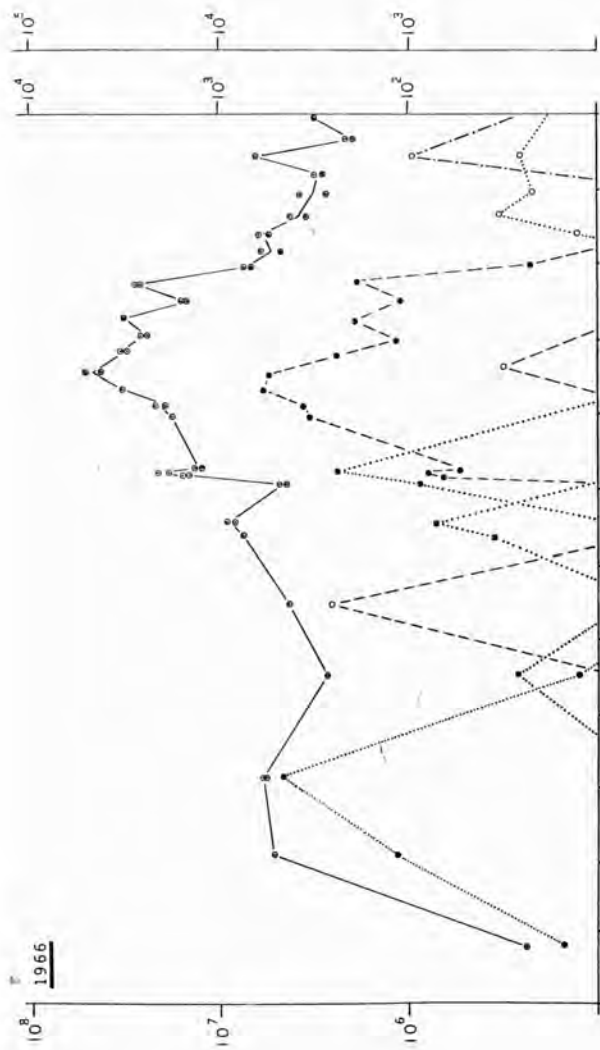


FIG. 9

(EVANS AND MCGILL)

See FIG. 17 in Thesis

FIG. 10  
(EVANS AND MCGILL)

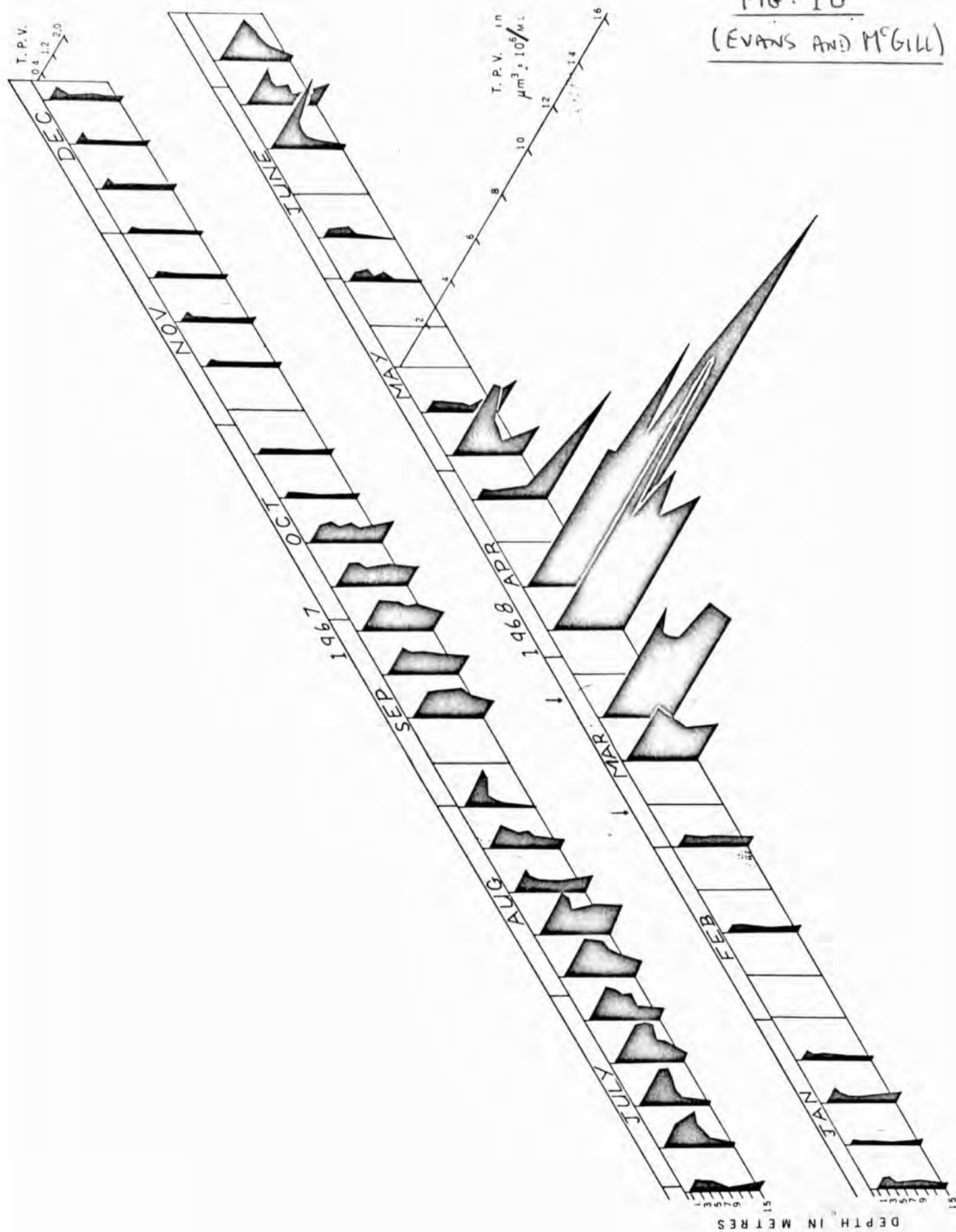
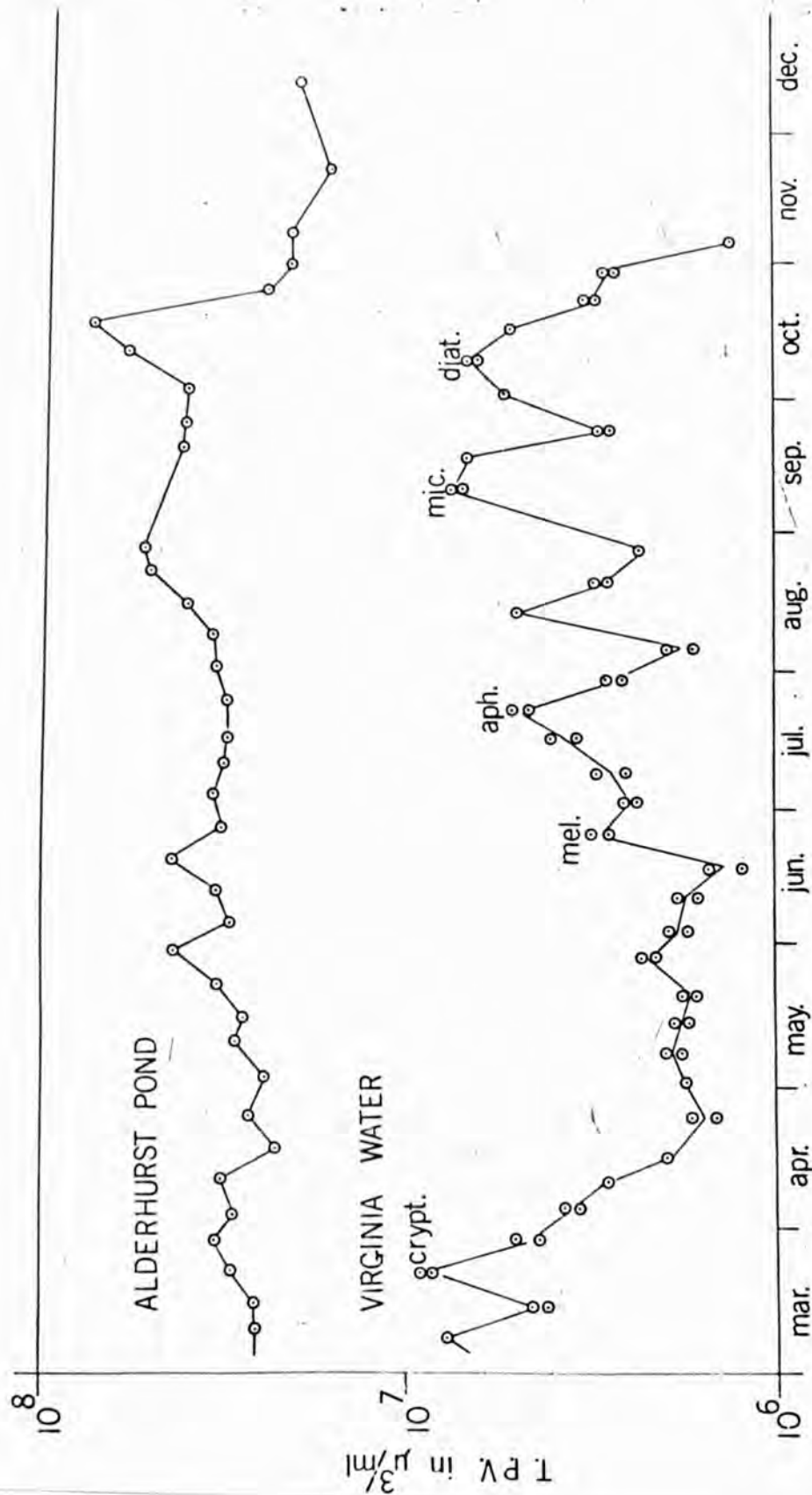


FIG. 11  
(EVANS AND M'GILL)



Miss S. M. MCGILL and Dr J. H. EVANS (Royal Holloway College)

**The determination of phytoplankton concentrations in a new reservoir by the Coulter Counter and other techniques**

During 1966, as part of an investigation of the phytoplankton flora of the Queen Elizabeth II reservoir (Metropolitan Water Board) which was constructed in 1962, an attempt was made to determine the possible use of the Coulter Counter in defining natural populations.

In conjunction with algal volumes computed from optical counts and measurements, the following determinations, mainly at weekly intervals, were made on the total seston: (1) total particulate volume (T.P.V.) by the Coulter Counter; (2) oven-dry weight at 60°C; (3) organic carbon by wet oxidation with potassium dichromate and sulphuric acid.

The relationship between these parameters depended upon the composition of the seston. When this consisted mainly of phytoplankton with one dominant species (e.g. *Fragilaria crotonensis* in July) or of one species of a distinctive size range in a mixture (e.g. *Coscinodiscus* sp. in a mixed population during October and November) these parameters, especially those of T.P.V. and calculated algal volume, were closely correlated. When the seston was composed mainly of silt and organic debris no such correlations could be shown but there was a relationship between T.P.V., organic carbon and dry weight.

The results suggest that the Coulter Counter may be extremely useful in conjunction with other methods in defining natural populations but less so as an instrument to be used alone for determining mixed phytoplankton.

*Br. phycol. Bull.* (1967) 3 (2) 411

## THE CARBON NUTRITION OF SOME ALGAE: THE INABILITY TO UTILIZE GLYCOLLIC ACID FOR GROWTH

By M. R. DROOP AND SUSANNE MCGILL<sup>1</sup>

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(Text-figs. 1 and 2)

Thirty-nine strains of (mainly) supra-littoral algae were tested for their ability to utilize glycollic acid for chemotrophic and phototrophic growth at the 'natural' pH of 8.0. In no instance was there convincing evidence that glycollate either supported growth in the dark or enhanced the growth rate in the light in the presence of carbon dioxide, although acetate performed one or both these functions in a number of the strains. It was concluded that glycollic acid was unlikely to serve as a significant carbon substrate in neutral or slightly alkaline habitats.

### INTRODUCTION

Glycollic acid has been much discussed since Tolbert & Zill identified it in the supernatants from *Chlorella* cultures in 1957. Pritchard, Griffin & Whittingham (1962) showed that it is excreted during photosynthesis mainly when carbon dioxide is the limiting factor. Fogg & Nalewajko (1964) found it in both fresh and marine waters and have demonstrated its uptake by algae. They suggested that the equilibrium between utilization and excretion of glycollate by algae may be an important ecological factor. They also suggested that it may be assimilated heterotrophically and so enable algae to survive periods of prolonged darkness. Indeed, survival and growth of phytoplankton under subarctic ice in winter (Rodhe, 1955) for example, or below the photic zone in the Mediterranean and elsewhere (Bernard, 1963), poses difficult problems. Can glycollic acid then support growth in darkness? Can its assimilation increase the growth potential in the light?

An organic acid such as glycollate might be utilized by an alga either as a major or as an accessory nutrient. When, as in the former case, the acid replaces carbon dioxide it might either be assimilated oxidatively and by-pass the photosynthetic cycle altogether (chemo-organotrophic growth) or it might be photosynthetically assimilated (photo-organotrophic growth). We have examined the ability of glycollate to promote the growth of a number of micro-algae, both in the light and in the dark. Since impermeability to organic solutes could cause an alga to be dependent for growth on carbon

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dioxide photosynthesis, we have included in our study several proved chemo- and photo-organotrophs which are permeable to acetate at least.

TABLE 1. SURVEY OF ACETATE AND GLYCOLLATE UTILIZATION

(The ability of these substances to enhance specific growth rate in the light or to support growth in the dark, based on optical comparisons of non-aerated cultures during the exponential phase. +, utilization definite;  $\pm$ , slight and doubtful; —, no evidence of utilization. Strain numbers (Millport collection) are shown in parentheses.)

	Phototrophy (1000 lux)		Chemotrophy (dark growth)	
	Acetate	Glycollate	Acetate	Glycollate
(19) <i>Balticola</i> ( <i>Haematococcus</i> ) <i>buetschlii</i>	+	$\pm$	—	—
(147) <i>B.</i> ( <i>Haematococcus</i> ) <i>buetschlii</i>	—	—	—	—
(165) <i>B. capensis</i>	$\pm$	$\pm$	—	—
(49) <i>B. droebakensis</i>	$\pm$	$\pm$	+	—
(42) <i>Brachiomonas submarina</i>	+	—	+*	—
(43) <i>B. submarina</i>	+	—	+*	—
(44) <i>B. submarina</i> var. <i>pulsifera</i>	+	—	+*	—
(45) <i>B. submarina</i> var. <i>pulsifera</i>	+	—	+*	—
(119) <i>Caulonema contortum</i> (nom. prov.)†	—	—	—	—
(11) <i>Chlamydomonas pulsatilla</i>	+	—	—	—
(120) <i>C. pulsatilla</i> var.	+	$\pm$	—	—
(150) <i>C. pulsatilla</i> var.	+	$\pm$	—	—
(151) <i>C. pulsatilla</i> var.	+	$\pm$	—	—
(152) <i>C. pulsatilla</i> var.	+	—	—	—
(153) <i>C. pulsatilla</i> var.	+	—	—	—
(175) <i>C. pulsatilla</i> var.	+	$\pm$	—	—
(176) <i>C. pulsatilla</i> var.	+	$\pm$	—	—
(67) <i>C. spreta</i>	+	—	+*	—
(68) <i>C. spreta</i>	+	—	+*	—
(116) <i>Chlorella ellipsoidea</i>	—	—	—	—
(57) <i>Dunaliella primolecta</i>	—	—	—	—
(31) <i>Hamatococcus pluvialis</i> (Cambridge)	+‡	—	+	—
(32) <i>Hamatococcus pluvialis</i> var. (Spitzbergen)	+‡	—	+	—
(40) <i>Hamatococcus pluvialis</i> var. (Finland)	+‡	—	+	—
(66) <i>Nannochloris oculata</i>	—§	—	—	—
(105) <i>Nannochloris</i> sp. (Lewin)	—	—	—	—
(118) <i>Stephanosphaera pluvialis</i>	+	$\pm$	+	—
(10) <i>Tetraselmis carteriaformis</i>	—	—	—	—
(115) <i>Tetraselmis</i> sp. (Cronulla)	—	—	—	—
(64) <i>Hemiselmis virescens</i>	—	—	—	—
(18) <i>Oxyrrhis marina</i>	—	—	+	—
(110) <i>Apisotonema</i> sp.	—	—	—	—
(62) <i>Cricosphaera elongata</i>	—	—	—	—
(58) <i>Isochrysis galbena</i>	—	—	—	—
(60) <i>Monochrysis lutheri</i>	—	—	—	—
(14) <i>Phaeodactylum tricornutum</i> (Finland)	—	—	—	—
(15) <i>Phaeodactylum tricornutum</i> (Plymouth)	—	—	—	—
(65) <i>Prymnesium parvum</i>	—	—	—	—
(73) <i>Skeletonema costatum</i>	—	—	—	—

\* Growth slow but repeatable, accompanied by loss of chlorophyll.

† Growth estimated visually. This alga probably belongs to the Ulotrichales.

‡ Probably chemotrophic.

§ Growth always very depressed.

## EXPERIMENTS

The culture medium was either *S* 50 (Droop, 1958) or *S* 66 (Droop, 1961), modified variously to meet individual minor nutrient requirements and with ammonium sulphate added for the dark experiments. The level of enrichment of acetate or glycollate was 1.0 g/l., the pH being set to 8.0 before autoclaving.<sup>1</sup> Growth was estimated optically in the preliminary survey, the results of which are shown in Table 1. More reliance can be placed on the chemotrophic than the phototrophic part of the table, since no effort was made to deplete the cultures of carbon dioxide. Thus, phototrophic assimilation can be expected to show only when the mechanism of carbon dioxide assimilation

TABLE 2. SPECIFIC GROWTH RATE OF SOME ACETATE UTILIZING ALGAE

(Log<sub>2</sub> increase per day with and without 1 g sodium acetate or glycollate per l. (95 % fiducial limits in parentheses). Conditions: test-tube cultures, not aerated, 1000 lux 'warm white' continuous fluorescent illumination. None of the *Chlamydomonas* strains showed any growth on either substrate in the dark. The medium for these strains contained lysine as N source.)

	Control	Glycollate	Acetate
	Growth in light		
(11) <i>Chlamydomonas pulsatilla</i>	0.39 ( $\pm 0.03$ )	0.40 ( $\pm 0.02$ )	1.75 ( $\pm 0.44$ )
(120) <i>C. pulsatilla</i> var.	0.36 ( $\pm 0.03$ )	0.39 ( $\pm 0.02$ )	0.77 ( $\pm 0.04$ )
(150) <i>C. pulsatilla</i> var.	0.42 ( $\pm 0.01$ )	0.36 ( $\pm 0.02$ )	0.54 ( $\pm 0.11$ )
(151) <i>C. pulsatilla</i> var.	0.59 ( $\pm 0.05$ )	0.71 ( $\pm 0.09$ )	1.33 ( $\pm 0.03$ )
(152) <i>C. pulsatilla</i> var.	0.39 ( $\pm 0.09$ )	0.37 ( $\pm 0.09$ )	0.96 ( $\pm 0.10$ )
(153) <i>C. pulsatilla</i> var.	0.90 ( $\pm 0.30$ )	0.63 ( $\pm 0.14$ )	1.23 ( $\pm 0.40$ )
(175) <i>C. pulsatilla</i> var.	0.67 ( $\pm 0.08$ )	0.47 ( $\pm 0.02$ )	0.68 ( $\pm 0.07$ )
(176) <i>C. pulsatilla</i> var.	0.45 ( $\pm 0.04$ )	0.51 ( $\pm 0.10$ )	0.69 ( $\pm 0.04$ )
(42) <i>Brachiomonas submarina</i>	0.66 ( $\pm 0.11$ )	0.64 ( $\pm 0.06$ )	1.30 ( $\pm 0.10$ )
(43) <i>B. submarina</i>	0.65 ( $\pm 0.03$ )	0.50 ( $\pm 0.03$ )	1.26 ( $\pm 0.08$ )
(44) <i>B. submarina</i> var. <i>pulsifera</i>	0.85 ( $\pm 0.15$ )	0.40 ( $\pm 0.01$ )	0.99 ( $\pm 0.18$ )
(45) <i>B. submarina</i> var. <i>pulsifera</i>	0.82 ( $\pm 0.04$ )	0.49 ( $\pm 0.06$ )	1.05 ( $\pm 0.06$ )
(31) <i>Haematococcus pluvialis</i>	0.64 ( $\pm 0.04$ )	0.72 ( $\pm 0.10$ )	1.08 ( $\pm 0.06$ )
	Growth in dark		
(31) <i>H. pluvialis</i>	0.0	0.0	0.82 ( $\pm 0.10$ )

is impaired to some extent, as for example in the *Chlamydomonas pulsatilla* and *Brachiomonas* cultures, or when growth is heavy enough to impose severe carbon dioxide limitation. Nevertheless, it is fairly clear that glycollate is not as good a substrate as acetate. There was not a single convincing instance of glycollate utilization, though there was the suggestion of it on the part of some of the 'acetate' Chlorophyta. More often glycollate depressed growth.

These comparative experiments provided little information about the early part of the growth curves and were sometimes difficult to interpret. We therefore repeated them with many of the 'acetate' strains, taking smaller

<sup>1</sup> At this pH the buffer capacity of the added acids is probably less than 1 % of the capacity of the glycylglycine and glycine already in the media, and any benefit due to enhanced uptake of carbon dioxide on account of the extra buffering action of the acids should be very small (Droop, 1966).

inocula and making cell counts from the second day onwards. The statistical analysis of the exponential phase counts is given in Table 2. Some variation is observed in the degree of dependence on photo-assimilation of acetate from strain to strain, and also on the amount of growth depression caused by the

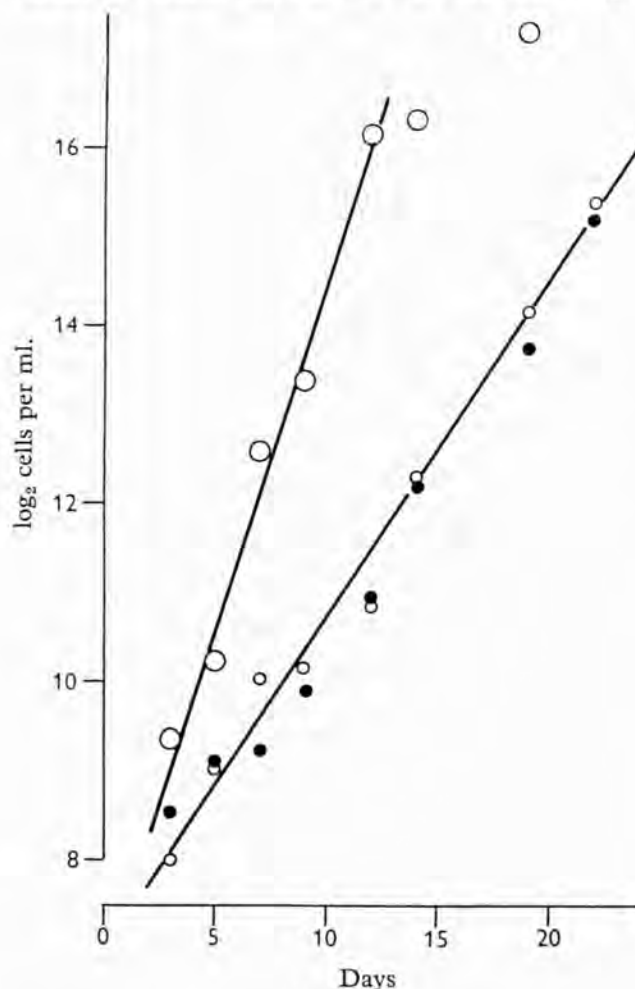


Fig. 1

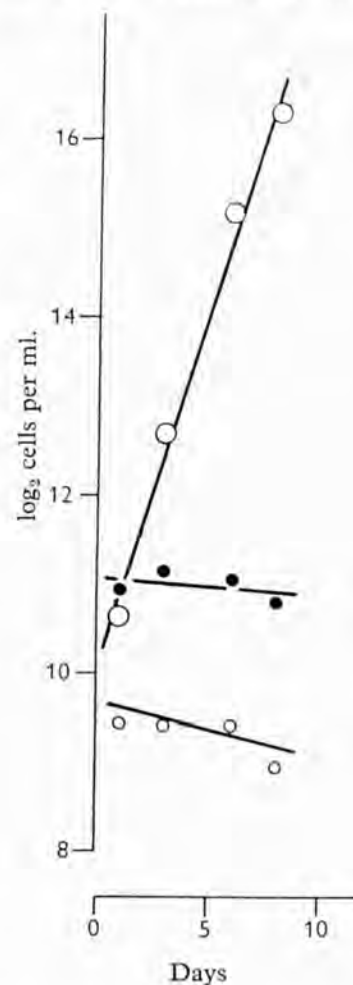


Fig. 2

Fig. 1. Growth of *Chlamydomonas pulsatilla* strain 120 in the light on lysine. Large circles with 1.0 g/l. sodium acetate; small circles, with 1.0 g/l. sodium glycollate; filled circles, with neither acid.

Fig. 2. Growth of *Haematococcus pluvialis* strain 31 in the dark on nitrate. Large circles, with 1.0 g/l. sodium acetate; small circles, with 1.0 g/l. sodium glycollate; filled circles, with neither acid.

glycollate addition; but, again, in no case did we find any evidence of significant growth enhancement with glycollate, although in two there was a slight increase on the control. The light curves for *Chlamydomonas pulsatilla* var. (120) and the dark curves for *Haematococcus pluvialis* (31) are shown in Figs. 1 and 2.

*H. pluvisialis* can utilize a number of acids for dark growth, including pyruvate, succinate, malate and glutarate, though none so readily as acetate. A very sensitive qualitative test for chemotrophic assimilation in this organism is the change in colour in the dark on agar slants due to carotinogenesis. The cultures are illuminated for a few days to allow some growth and then while still green placed in the dark. It was possible thus to show that even citrate and tartate were assimilated to some extent though they did not support growth.<sup>1</sup> Assimilation of glycollic acid could not be demonstrated by this method.

There is the possibility that glycollate could serve as a respiratory substrate but without contributing by itself sufficient energy to support growth. However, we showed that it did not 'spare' carbon dioxide, though acetate presumably did so in a number of cases (Table 2). The following comparison of specific growth rates during dark growth of *H. pluvisialis* (31) shows there is no sparing action of 1.0 g/l. sodium glycollate on the same quantity of acetate in this species:

Acetate alone	0.75 (limits, $\pm 0.16$ )
Acetate and glycollate	0.72 (limits, $\pm 0.08$ )

Previously *Chlamydomonas pulsatilla* was reported to have an absolute requirement for acetate in the light (Droop, 1961), erroneously as it now proves. Evidently the ability of some of these algae to assimilate carbon dioxide is not too assured<sup>2</sup> and depends to some extent on culture conditions. Variation in pH, for instance, affects both the supply of carbon dioxide and the penetrating power of organic acids. Something of this can be seen in the variation in specific growth rate during the exponential phase with the medium pH setting in *Brachiomonas* (Table 3).

TABLE 3. EFFECT OF INITIAL pH ON SPECIFIC GROWTH RATE OF *BRACHIOMONAS SUBMARINA* STRAIN 42

(During the first week of exponential growth in the presence and absence of 1.0 g/l. sodium acetate or glycollate. (Medium S 66).)

pH	7.0	8.0	9.0
Acetate	0.85	1.26	1.14
Glycollate	0.83	0.97	0.94
Control	0.95	1.10	0.95

#### DISCUSSION

The cell is presumably permeable to substances excreted. Therefore, if glycollate excretion by algae is of general occurrence impermeability cannot account for the negative results reported here. Wiessner & Kuhl (1962) and Wiessner (1965) have suggested that the acetate conversion to carbohydrate,

<sup>1</sup> Droop, M. R., Ph.D. Thesis, University of Cambridge, 1954.

<sup>2</sup> See Pringsheim & Wiessner (1961) on *Chlamydomonas*, *Euglena*, *Chlorogonium* and *Chlorella*.

by incorporation (in the form of acetyl coenzyme A) into the glyoxalate cycle, utilizes ATP phosphorylated either oxidatively or photosynthetically as the case may be. Evidently this pathway is not open to hydroxyacetic acid.

The finding that glycollate is unable to support growth, at least in the range of algae we have tested, does not however invalidate Fogg's hypothesis concerning the wastage of an essential intermediate by excretion (Fogg & Nalewajko, 1964). But it does seem that this acid is unlikely to make a significant nutritional contribution to algal growth either in the light or the dark in neutral or slightly alkaline waters. Organic acids, on the other hand, act as pH buffers and may materially influence growth without being metabolized in any way, especially when the environment is unpoised and without excess of hydroxyl ions (Droop, 1966).

As a final word, the species represented in our survey are drawn largely from brackish supra-littoral rock pools and are hardly typical of phytoplankton, for example, for they include a very high proportion of 'myxotrophic' types. On the other hand, the ability to grow with glycollic acid is more likely to be met here where the tendency to diversity in nutrition already exists than among the less versatile pelagic forms.

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